A PRELIMINARY CONSPECTUS OF THE ALLON FLORA FROM THE LATE CRETACEOUS (LATE SANTONIAN) OF CENTRAL GEORGIA, U.S.A.[1]

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ABSTRACT

A preliminary conspectus of the fossil flora from the Allon locality, in Crawford County central Georgia, documents the presence of at least 63 distinct plant organs, based on macrofossils and mesofossils, but excluding dispersed pollen and spores. The fossils are preserved in a clay lens within the Buffalo Creek Member of the Gaillard Formation, and are of late Santonian (Late Cretaceous) age. In general, macrofossils are sparse at this site, but abundant mesofossils have been isolated from bulk samples by sieving. The flora includes sporophytes and gametophytes of fossil mosses (e.g., *Eopolytrichum antiquum, Campylopodium allonense*), ferns (e.g., cf. *Boodlepteris*), and conifers, but is dominated by the diverse and abundant remains of angiosperms. Angiosperms in the flora include cf. *Detrusandra* (Magnoliales), *Mauldinia* sp. (Lauraceae), *Allonia decandra* (Hamamelidaceae), and *Parasaurauia allonensis* (Actinidiaceae). Especially abundant are flowers and cupules of two species of Fagaceae sensu lato (*Protofagacea allonensis, Antiquacupula sulcata*). The flora also includes fossil flowers of *Caryanthus* sp. (Juglandales/Myricales) and *Bedellia pusilla* (cf. Betulaceae), which comprise the first record of Normapolles-producing flowers from North America. The structural and systematic diversity of angiosperms in the Allon flora is comparable to that at other Turonian-Campanian sites in eastern North America and Europe. Together, these fossil floras indicate that angiosperms, and especially eudicots, were already diverse at this relatively early stage in angiosperm evolution. The source vegetation represented by the Allon fossil assemblage was dominated by angiosperms, probably with taxodiaceous conifers also common. Preservation of most of the mesofossils as charcoal indicates that fire may have been an important factor contributing to frequent disturbance of the source plant community.

Over the last two decades, investigations of Cretaceous floras have been revitalized by the emergence of a wealth of new paleobotanical data and the application of a more rigorous approach to the comparison of Cretaceous fossil plants with their living relatives. Especially striking have been rapid advances in the study of mesofossil assemblages isolated from plant debris beds, which have included remarkable discoveries of fossil flowers, and other small, delicate, plant fossils (e.g., moss gametophytes and sporophytes) that have not been recognized previously. Mesofossil assemblages are generally obtained by wet sieving and panning of unconsolidated sediments that can be disaggregated in water. Typically, they are comprised of three-dimensionally preserved fossils 0.5–5 mm in maximum dimension: too small to be seen easily in the field and too large to survive standard palynological preparation techniques.

Mesofossil assemblages from the Cretaceous have yielded extremely well-preserved angiosperm flowers, fruits, seeds, stamens, and wood, as well as cones, pollen organs, and wood of other seed plants (especially conifers), fern pinnules and rhizomes, remains of other pteridophytes, and bryophyte sporophytes and gametophytes. Specimens may be lignified or charcoalified, and both modes of preservation can be studied easily with scanning electron microscopy to reveal morphological and anatomical information. Charcoalified specimens,

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in particular, are often exquisitely preserved and yield a level of fine structural detail comparable to that obtained from extant plants.

Studies of mesofossils have greatly expanded our knowledge of previously described plant fossils (e.g., *Eucommiidites*-producing plants, Pedersen et al., 1989) and have provided new insights into the diversity and systematic relationships of Cretaceous angiosperms (e.g., Crane et al., 1989, 1994, 1995; Crepet & Nixon, 1994, 1996, 1998; Friis, 1984, 1985, 1990; Friis & Skarby, 1982; Friis et al., 1986, 1988, 1995, 1997a; Gandolfo et al., 1998a, b; Herendeen, 1991a, b; Herendeen et al., 1994, 1995; Keller et al., 1996; Magallón-Puebla et al., 1996, 1997; Pedersen et al., 1991, 1994; Sims et al., 1998). In addition, because pollen is frequently preserved in situ within mesofossil reproductive structures, these studies have led to the identification of the parent plants of many Cretaceous angiosperm pollen grains that were previously only known from dispersed palynofloras (Friis, 1983; Crane et al., 1989; Pedersen et al., 1989, 1991; Sims et al., 1999).

The impact of research on mesofossils has been especially pronounced in changing our understanding of the Cretaceous fossil history of flowering plants. New discoveries, especially from the Late Cretaceous of Europe and eastern North America, have substantially extended the known fossil record of many angiosperm groups (e.g., Herendeen et al., 1995; Sims et al., 1998) and have documented the presence of many lineages that previously were not known to have a reliable fossil record (Friis et al., 1997b; Magallón-Puebla et al., 1999). Information on fossil flowers has provided new insights into floral architecture, pollination, and dispersal in extinct angiosperms, and how these structural and biological features may have changed through time. Morphological and systematic studies of mesofossils have yielded new information on the fossil history of bryophytes (Konopka et al., 1997, 1998), ferns (Gandolfo et al., 1997b; Herendeen & Skog, 1998), conifers (Srinivasan, 1992, 1995; Srinivasan & Friis, 1989), and other gymnosperms (Pedersen et al., 1989, 1993). Paleoecological studies based on mesofloras are also contributing valuable new information for interpreting Cretaceous vegetation (Lupia, 1994, 1997).

Mesofossil assemblages have been described from sediments in North America and Europe that range in age from Barremian-Aptian to Maastrichtian. In Europe, the most intensively studied site is the Åsen locality in Scania, southern Sweden (e.g., Friis & Skarby, 1982; Friis, 1983, 1984, 1985, 1988, 1990), which includes a large number of different assemblages that are of late Santonian to early Campanian age. Other mesofossil assemblages have been recovered from the Early Cretaceous of southern England (e.g., Herendeen & Skog, 1998), and many localities in the Late Cretaceous of central Europe (Knobloch & Mai, 1984, 1986, 1991). Also intensively studied are a sequence of rich mesofossil assemblages from the Cretaceous of western Portugal that have yielded important data on early angiosperm evolution and that range from Barremian-Aptian to Maastrichtian in age (e.g., Friis et al., 1992, 1994, 1999). In Asia, important mesofossil assemblages are known from the Coniacian-Santonian of Japan (Takahashi, Crane & Ando, in prep.) and the Cenomanian-Turonian of Kazakhstan (Frumin & Friis, 1996, 1999).

In North America the most intensively studied mesofossil localities are from the Cretaceous of the Atlantic Coastal Plain, where a series of floras are known from Martha's Vineyard (Tiffney, 1977) and New Jersey (e.g., Crepet & Nixon, 1994; Gandolfo et al., 1997b) in the north, to central Georgia in the south (Crane & Herendeen, 1996; Crane et al., 1994; Friis et al., 1986, 1988, 1997a). These fossil assemblages range in age from Aptian to Campanian and are continuing to yield a great diversity of well-preserved mesofossil material (e.g., Crane & Herendeen, 1996). Other mesofossil floras from the Great Plains and Rocky Mountain regions of North America have been less intensively studied than those in eastern North America and in general they appear less well preserved (Herendeen, unpublished).

Most studies of mesofossils published to date have presented detailed treatments of the morphology and systematic relationships of particular fossil taxa. This approach has drawn attention to some of the most common components of mesofossil assemblages and has clarified fossil history of many groups of angiosperms and other plant lineages. However, a by-product of this focused approach has been that only a small fraction of the total plant diversity preserved as mesofossils has been described. Complete paleofloristic descriptions that illustrate and describe the diverse structures in a single mesofossil assemblage using modern techniques, and that also include both the angiosperm and non-angiosperm components of these floras, have not been presented.

In this paper we present a preliminary conspectus of the Allon flora: a diverse and well-preserved late Santonian (Late Cretaceous) mesofossil assemblage from central Georgia. Several other diverse mesofossil assemblages from Georgia are currently under investigation, but the Allon flora has been

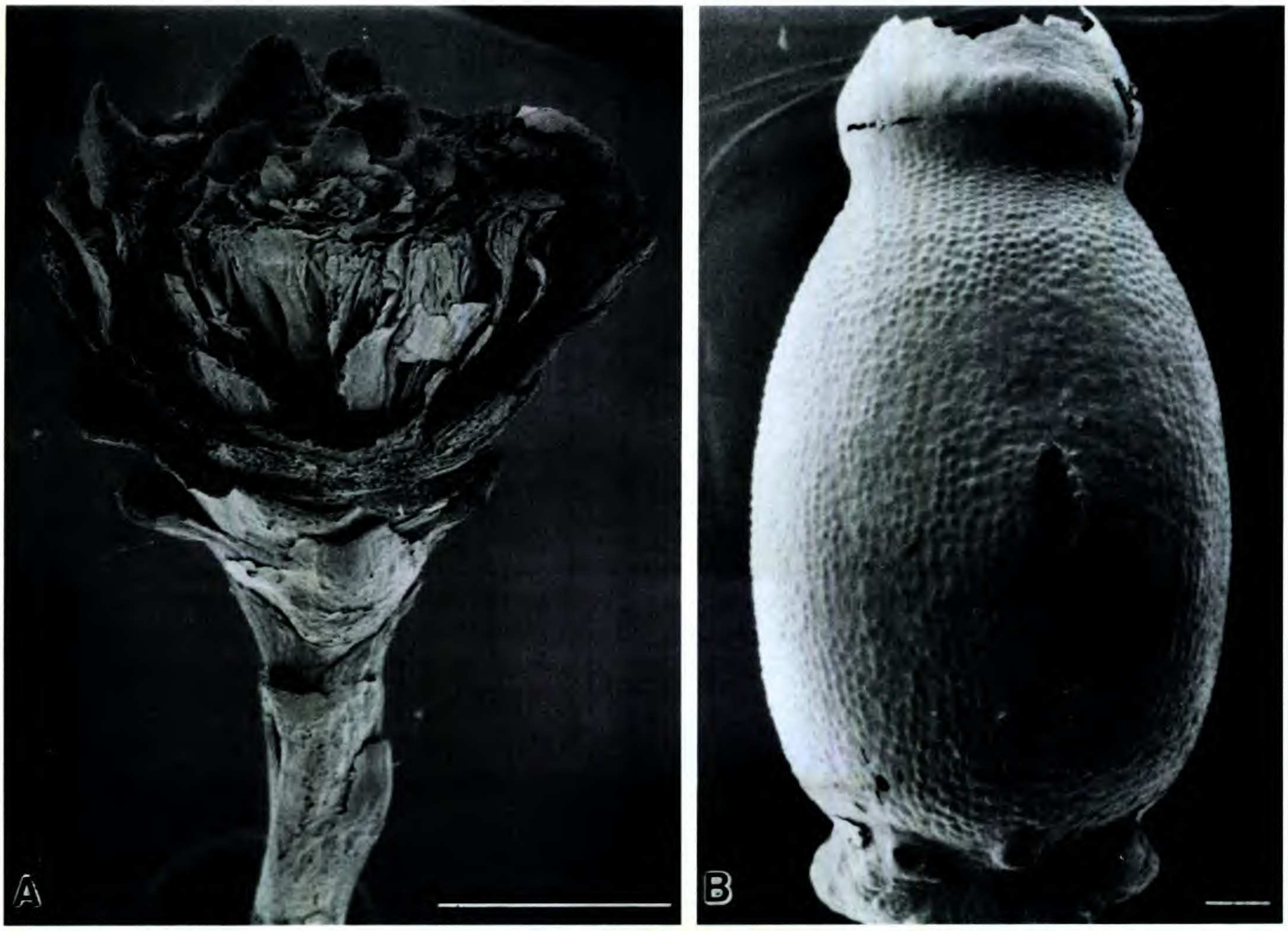

Figure 1. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 1, *Eopolytrichum antiquum* Konopka, Herendeen, Smith Merrill & Crane (Polytrichaceae). —A. Oblique view of fertile gametophyte shoot apex showing elongated antheridia and numerous leaves with photosynthetic lamellae on their adaxial surface; PP44724. —B. Lateral view of sporophyte capsule showing the line of separation of the operculum, swollen apophysis at the base and prominent stomata; PP44717. Scale bars; A = 1 mm. B = 100 μm.

studied for several years, and several detailed treatments of specific taxa are already published (Crane & Herendeen, 1996; Herendeen et al., 1995; Keller et al., 1996; Konopka et al., 1997, 1998; Magallón-Puebla et al., 1996; Sims et al., 1998, 1999). Most taxa from the Allon flora, however, have not yet been described. Some components of the mesofossil assemblages have not been treated because they belong to plant groups that are not yet the focus of a major research effort (e.g., conifers), while in other cases there has been insufficient material to prepare a detailed description that could serve as the basis for systematic analysis. For many angiosperm mesofossils, uncertainty over systematic relationships has also served as a disincentive for publication.

To our knowledge, the treatment of the Allon flora in this paper is the first time that a Cretaceous mesofossil assemblage has been documented in its entirety based on scanning electron microscopy. Preliminary descriptions and photographs (excluding details of anatomy and pollen/spores for reasons of space) are presented of all bryophyte, fern, conifer, and angiosperm mesofossil remains that we have been able to discriminate and characterize. Only the dispersed pollen and spores, as well as a small number of poorly preserved dispersed seeds, stamens, and coprolites, are not treated. We also provide documentation of the leaf impression/compression fossils that are known from the Allon locality, and present an initial estimate of the relative abundance of the different elements in the mesofossil assemblage. A preliminary estimate of the relative diversity of different major plant groups in the flora is also provided.

Future research on the Allon flora will undoubtedly result in the recognition of new taxa. In the meantime, however, the preliminary conspectus presented here will provide useful data for comparison with other mid and late Cretaceous mesofossil localities (Lupia, work in progress) and will help place the diversity of late Santonian angiosperms in a broader context that includes other elements of Late Cretaceous vegetation.

MATERIALS AND METHODS

The fossil material described here was collected from a clay lens in the south pit ("Allon" quarry) of the Atlanta Sand and Supply Company (Knoxville Quadrangle, lat. 32°37′47″N, long. 83°59′10″W) in Gaillard, Georgia, ca. 9.5 km southeast of Roberta in Crawford County. The clay lens has been assigned to the Buffalo Creek Member of the Gaillard Formation (Huddlestun & Hetrick, 1991). The Buffalo Creek Member is considered to be of late Santonian age. This is based on the presence of terrestrial palynomorphs that are considered to be biostratigraphically equivalent to those in marine units assigned to the late Santonian based on calcareous nannofossils (i.e., equivalent to the lower part of calcareous nannofossil zone CC17, which Burkett [1996] considered to be late Santonian) (Christopher, unpublished data).

The clay lens yielding the mesofossils varies from 0.2 to 0.8 m thick, is truncated at both ends, and has a lateral extent of at least 16 m in the outcrop. The clay is microlaminated, dark gray, and carbonaceous. It is inferred to represent a lower floodplain pond, and the presence of rare dinoflagellates in the palynoflora perhaps indicates some tidal influence (Lupia & Sims, unpublished). In terms of the mesofossils, the productivity of the Allon locality varies across the outcrop from about 250 specimens per 20-kg sample where the lens is thick, to about 2500 specimens per 20-kg sample at the extreme edge where the lens is thinnest. There is also considerable variation in the composition of the mesofossil assemblage among different samples (Lupia, 1997; in prep.). The Allon flora contains a diverse assemblage of angiosperms, gymnosperms, ferns, and bryophytes preserved as fusainized and lignitic mesofossils (Herendeen et al., 1995; Crane & Herendeen, 1996; Keller et al., 1996; Magallón-Puebla et al., 1996; Konopka et al., 1997, 1998; Sims et al., 1998, 1999). The clay also contains a macrofossil assemblage, which is preserved as impressions or thin compressions, and a diverse palynoflora.

The material was prepared by dissolving bulk samples of clay in water and then washing the slurry through a series of sieves (finest mesh 125 μm). Isolated plant material was cleaned with HCl, followed by HF, and then thoroughly washed in water. The fossil material was air-dried and examined using a binocular stereomicroscope. Specimens picked from the organic debris were mounted on stubs, coated with gold, and examined with an Amray 1810 scanning electron microscope. After initial scanning, selected specimens were partially dissected to reveal internal morphology, and then recoated and scanned. Except where noted all illustrations are scanning electron micrographs. All fossil specimens are deposited in the paleobotanical collections of the Department of Geology, The Field Museum, Chicago (PP).

DESCRIPTIONS AND DISCUSSION OF FOSSIL PLANTS

MOSSES

Polytrichaceae

1. *Eopolytrichum antiquum* Konopka, Herendeen, Smith Merrill & Crane
   Figure 1.

Sporophyte capsules are terete to somewhat dorsiventrally flattened in cross section, 0.9–1.1 mm long, 0.6–0.8 mm wide, and have a swollen, asymmetrical apophysis and mammillose exothecium. Stomatal complexes, each surrounded by a ring of subsidiary cells, are confined to the apophysis (Fig. 1B). The operculum is tall and dome-shaped, but the calyptra and beak of the operculum are not preserved. Remains of a peristomial membrane are present around the rim of the capsule after the operculum has dehisced, but peristome teeth are absent and the epiphragm is retained in the operculum. Spores are alete, spherical, and echinulate (Konopka et al., 1997). Associated sterile and fertile male (Fig. 1A) gametophytes have leaves with adaxial, presumed photosynthetic, lamellae on the blade surface as well as other anatomical structures comparable to those of leaves in extant Polytrichaceae.

The structure and relationships of *Eopolytrichum antiquum* were described by Konopka et al. (1997).

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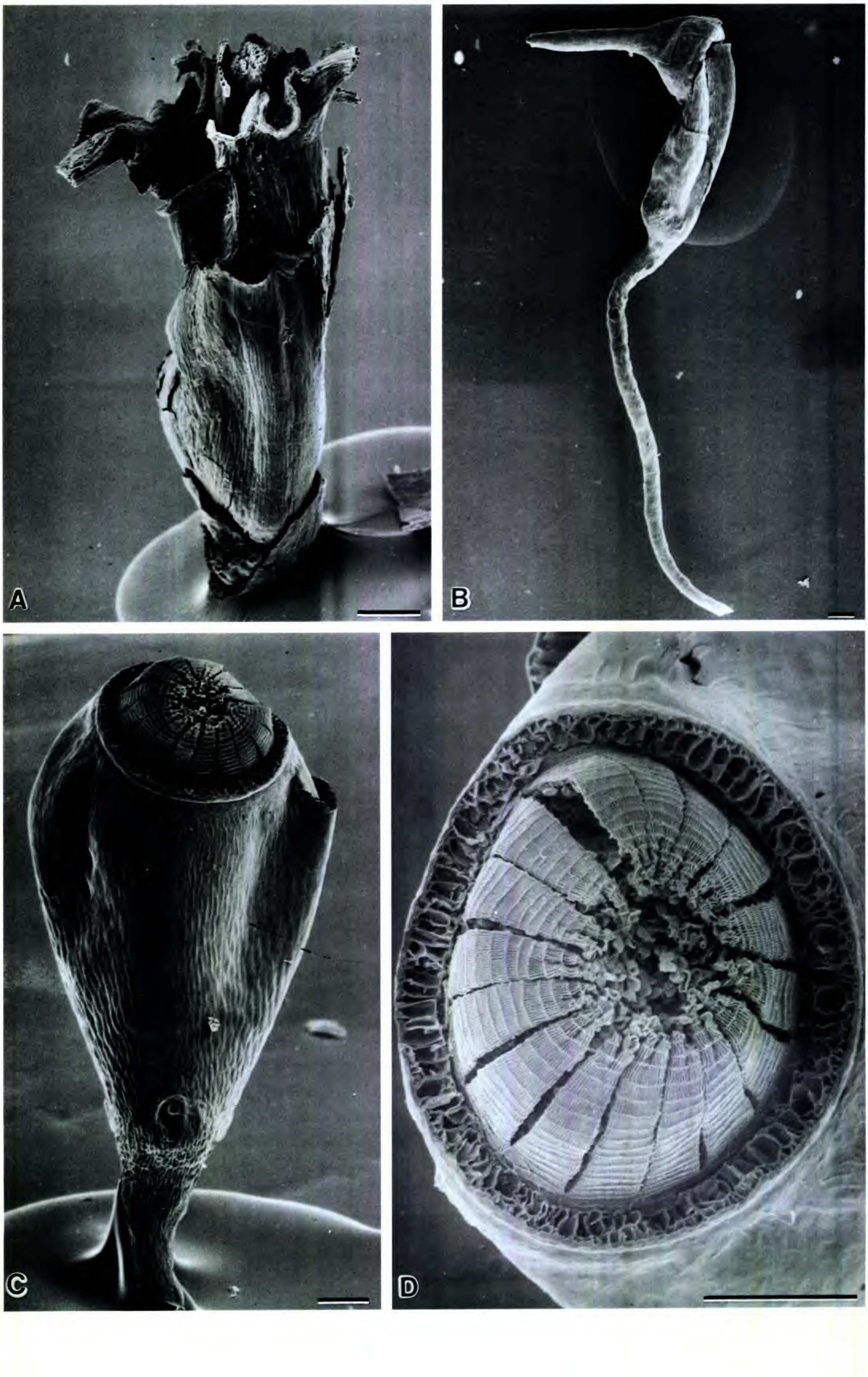
Figure 2. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 2, *Campylopodium allonense* Konopka, Herendeen & Crane (Dicranaceae). —A. Lateral view of gametophyte axis fragment showing leaves with broadly sheathing bases and abruptly narrowed blades; PP44740. —B. Lateral view of sporophyte capsule showing attached seta, slightly swollen apophysis, prominent stomata and cuculate operculum; PP45163. —C. Lateral view of sporophyte capsule showing narrowed base, prominent stoma and attachment to the seta; operculum missing and exposing the peristome teeth; PP44725. —D. Apical view of peristome showing compound annulus, teeth with divided tips and numerous spores in the center; PP44725. Scale bars = 100 μm.


A
B
C
D

Morphological and anatomical details clearly indicate that the fossil sporophytes belong to the family Polytrichaceae, but the combination of features in the fossils does not occur in any extant genus (Konopka et al., 1997; Table 1). Associated fossil gametophytes exhibit the distinctive lamellae and leaf anatomy of the Polytrichaceae, and the male gametophytes contain characteristic clavate paraphyses and antheridia. Toothed leaf margins and pyriform marginal cells of lamellae occur in several extant genera of Polytrichaceae, but the rounded abaxial protuberances of the leaf sheath are unique to the fossil. More detailed information is needed about the epiphragm, columella, peristomial membrane, and tooth structure in extant taxa in order to determine structural homologies within and among Polytrichales, Bryales, Tetraphidales, and other major lineages of mosses. A more precise understanding of the relationships of *Eopolytrichum* within the Polytrichaceae will require cladistic analysis that includes the fossil and relevant extant taxa.

Eopolytrichum antiquum is known from two sporophyte capsules and four gametophyte specimens.

Dicranaceae

2. *Campylopodium allonense* Konopka, Herendeen & Crane
   Figure 2.

Fossil sporophyte capsules are curved, cylindrical, and strumose (Fig. 2B), 1.7–2.4 mm long, with an obliquely rostrate operculum (Fig. 2C), cucullate calyptra, and compound annulus (Fig. 2D). The peristome is haplolepidous with 16 dicranoid, apically bifid teeth that are vertically striate on the outer surface (Fig. 2D) and asymmetrically trabeculate on the inner surface. Spores are alete, spherical, and finely rugose, and thus differ from the finely papillose spores of extant *Campylopodium* (Konopka et al., 1998). Spores identical to those found within the sporangium have been found on the leaf surfaces of one of the gametophyte specimens, providing circumstantial evidence that both sporophyte and gametophyte belong to the same species. Fossil gametophytes are consistent with the morphology of extant *Campylopodium* and have leaves with a broad sheathing base and a narrow blade (Fig. 2A).

Sporophytes and gametophytes of *Campylopodium allonense* were described by Konopka et al. (1998). *Campylopodium allonense* represents the first appearance of Dicranaceae in the fossil record. This material, along with *Eopolytrichum antiquum* also from the Allon locality, represents two different subclasses of mosses, and provides the first definitive evidence of modern families of mosses in the Cretaceous. In a phylogenetic context, these fossils imply that mosses were already diverse at the family and genus level by the Late Cretaceous.

Campylopodium allonense is represented in the Allon flora by ca. 20 sporophyte capsules and at least 10 gametophyte specimens.

FERNS

Gleicheniaceae

3. cf. *Boodlepteris* Gandolfo, Nixon, Crepet & Ratcliffe
   Figure 3.

Ultimate pinnules are alternate, sessile, and broadly rounded to obtuse, 0.5 mm long, 0.7 mm wide (Fig. 3A, B). The midvein does not reach the apex of the pinnules, and lateral veins are not evident (Fig. 3B). The ultimate rachis is slightly sinuous (Fig. 3A). Fertile specimens have not been found.

Only two specimens of these fern pinnule fragments are known and both are similar to those of *Boodlepteris turoniana* Gandolfo, Nixon, Crepet & Ratcliffe (1997b) from a Turonian age locality (lower Magothy Formation) in Sayreville, New Jersey (Old Crossman Clay Pit). Fertile specimens have not been found at the Allon site, but the Turonian material bears exindusiate sori composed of 10–20 sporangia (Gandolfo et al., 1997b). Based on cladistic analysis, *Boodlepteris turoniana* is thought to be most closely related to the extant genus *Stromatopteris* (Gleicheniaceae) (Gandolfo et al., 1997b). Another fossil representative of Gleicheniaceae was described by Herendeen and Skog (1998) based on charcoalified pinnule fragments from a mesofossil assemblage in the Early Cretaceous of Bedfordshire, England. These fossils were described as an extinct species of the extant genus *Gleichenia*. The extensive fossil record of the family Gleicheniaceae is reviewed by Herendeen and Skog (1998).

Fern, family *incertae sedis*

4. Fern leaf type 1
   Figure 4.

Leaf fragments are pinnate with ultimate pinnules alternate, sessile, narrowly triangular, and with an acute apex, 3 mm long, 1.5 mm wide at base (Fig. 4A–C). Presumed mature pinnules are more broadly triangular (Fig. 4D) and have revolute margins, and the midvein is raised on the abaxial side (Fig. 4E). Stomata have not been observed.

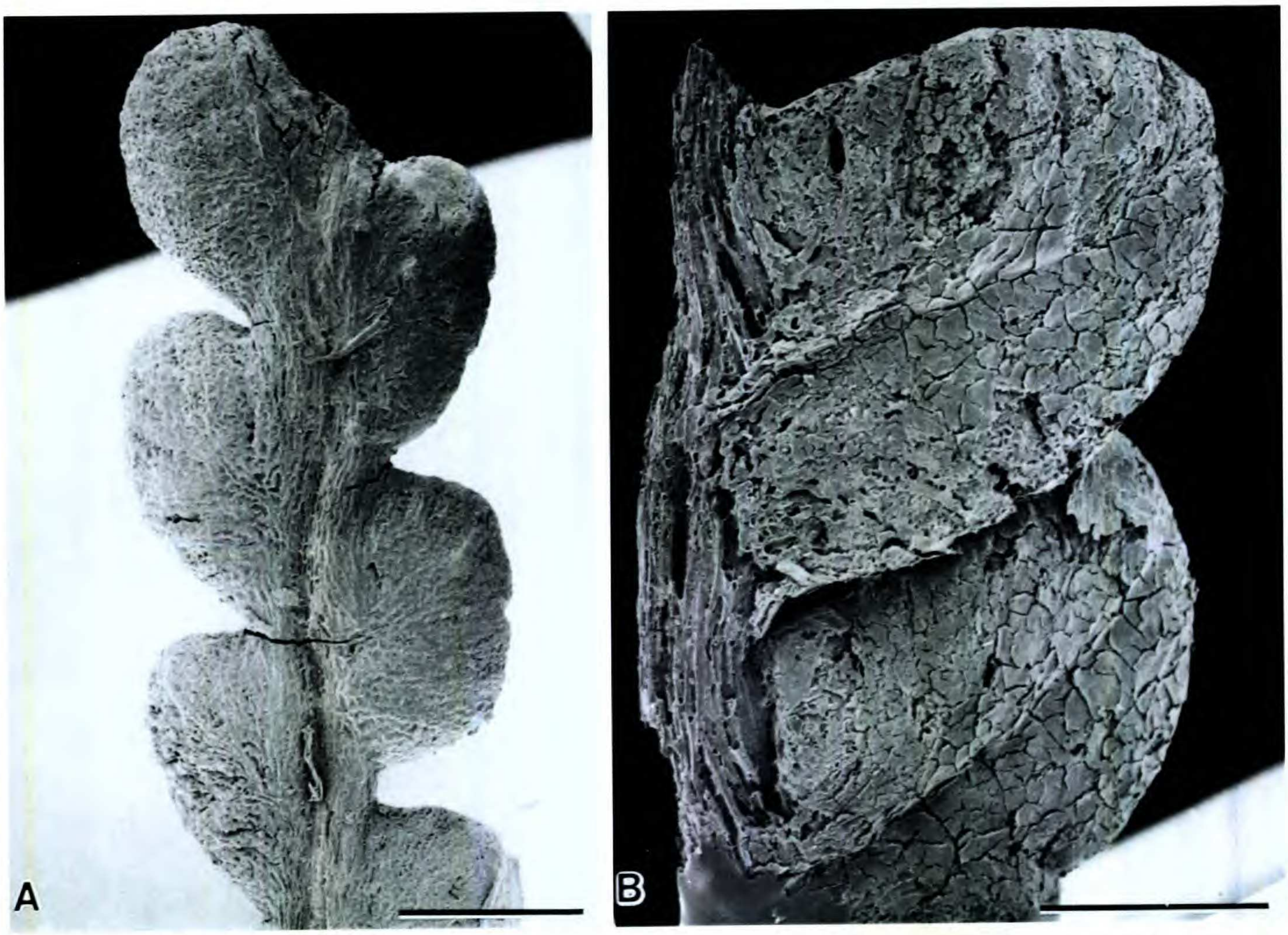


Figure 3. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 3, cf. *Boodlepteris* Gandolfo, Nixon, Crepet & Ratcliffe (Gleicheniaceae). —A. Fern pinna with alternate, rounded pinnules; PP45158. —B. Fern pinna with alternate, rounded pinnules; PP45159. Scale bars = 0.5 mm.

Only sterile specimens are known. Simple trichomes are abundant on the abaxial leaf surface. Rachis and rhizome anatomy are unknown.

The available details are insufficient to evaluate the affinities of these few fragmentary specimens. Specimens of fern leaf type 1 are rare in the Allon fossil assemblage.

5. Fern leaf type 2 (macrofossil)
   Figure 5A.

Leaf fragment pinnatifid, 20 mm long. Proximal pinnules broadly triangular with 1–2 teeth. Distal pinnules narrowly triangular and lacking teeth. Details of pinnule venation not preserved.

This single fragment, of unknown systematic relationships, is the only evidence of ferns in the Allon macroflora. The specimen is similar to pinnules of *Dryopterites stephensonii* Berry (1914, pl. 17, fig. 1) from the Eutaw Formation (Santonian-Campanian) of Georgia, but the absence of pinnule venation in the Allon material precludes more detailed comparison.

CONIFERS

Conifers, family *incertae sedis*

6. Conifer foliage type 1 (cf. *Brachyphyllum* Brongniart) (macrofossil)
   Figure 5B.

Branched, planated conifer leafy shoot bearing numerous, tightly appressed, helically arranged scale leaves with acute apices. Shoots up to 3–4 mm wide.

Only a single fragment of this conifer leaf shoot has been found. In overall form it resembles leafy shoots often assigned to *Brachyphyllum* and assumed to be of araucariaceous or cheirolepidiaceous affinity. In this context it may be significant that *Classopollis* pollen (Cheirolepidiaceae) has not been detected in the Allon palynoflora. The specimen resembles shoots from the Allon mesoflora assigned to conifer foliage type 4 (taxon 9).

7. Conifer foliage type 2 (macrofossil)
   Figure 5C.

Conifer leafy shoot bearing helically arranged, acicular, leaves up to 5 mm long, with pointed api-

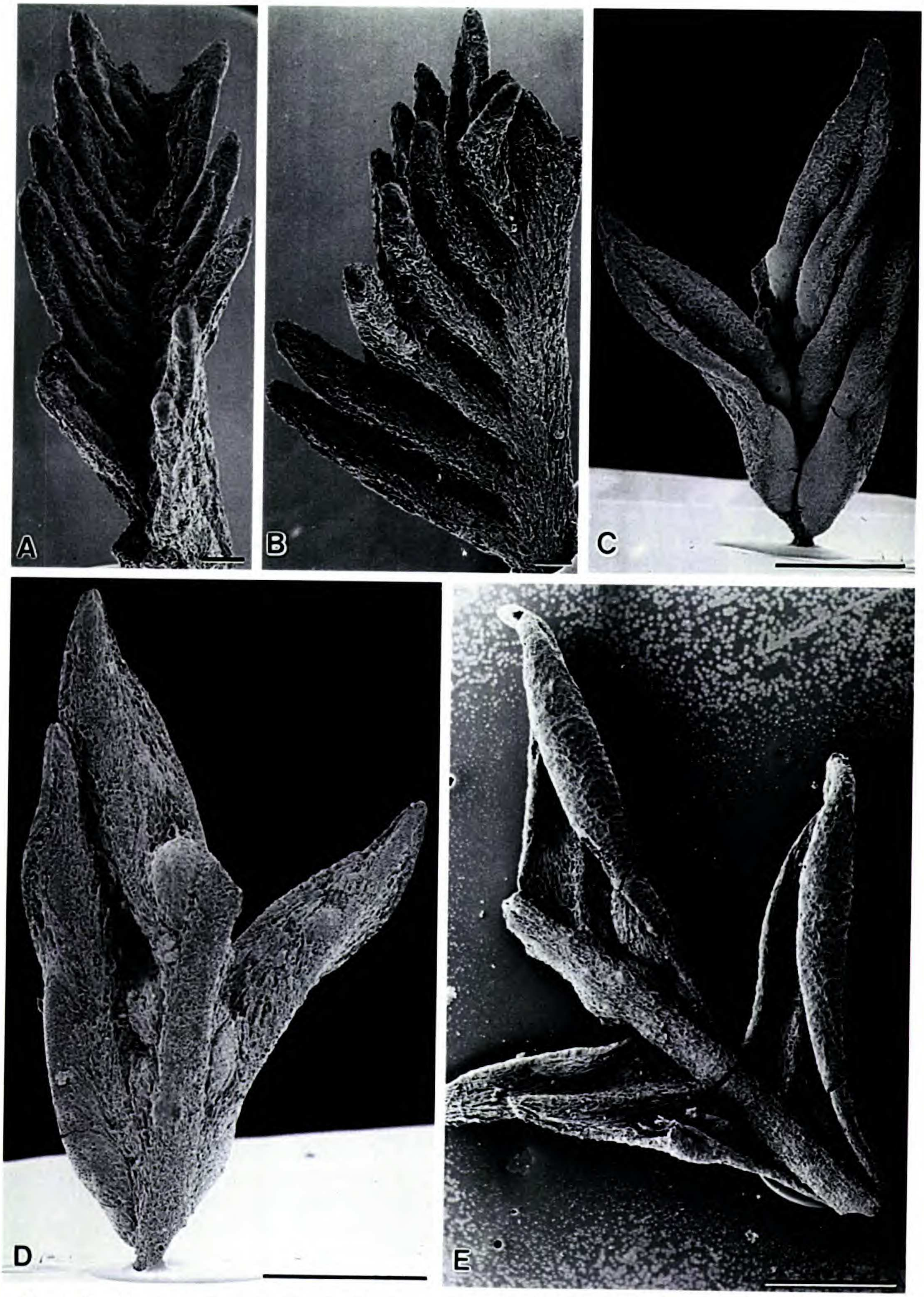


Figure 4. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 4, Fern leaf type 1. —A. Frond fragment with alternate, narrowly triangular acute pinnules; PP45160. —B. Abaxial surface of specimen shown in A. —C. Frond fragment with alternate, acute pinnules, showing the abaxial surface; PP45161. —D. Adaxial surface of specimen shown in C. —E. Fern with alternate, acute pinnules, showing the adaxial surface with a prominent rachis and pinnule midvein; PP45162. Scale bars; A, B = 100 μm. C, D, E = 1 mm.

Figure 5. Macrofossils from the Allon locality, Georgia (late Santonian; Late Cretacous): Taxa 5, 6, and 7, Ferns and conifers; light micrographs. —A. Taxon 5, Fern leaf type 2, frond fragment showing pinnules, macrofossil; PP45376. —B. Taxon 6, Conifer foliage type 1 (cf. *Brachyphyllum*), shoot bearing numerous scale-like leaves, macrofossil; PP4537. —C. Taxon 7, Conifer foliage type 2, shoot bearing elongated leaves, macrofossil; PP45378. Scale bars = 10 mm.

ces. Many fragments of this conifer leafy shoot have been found. Among the conifers described by Berry (1914) from the Santonian-Campanian of Georgia, the Allon material is most similar to the specimens described as *Sequoia reichenbachi* (Geinitz) Heer, but the absence of anatomical information for both the Allon material and the specimens illustrated by Berry (1914, pl. 4) precludes more detailed comparison. Isolated conifer leaves (Fig. 6F) similar to those of conifer foliage type 2 are described below under conifer foliage type 3 (taxon 8).

cf. Taxodiaceae

8. Conifer foliage type 3
   Figure 6.

The material consists of a variety of leafy shoots (Fig. 6A–E) and isolated leaves (Fig. 6F). The leaves have an acute apex and decurrent base, and when observed attached are helically arranged. Some leaves have parallel margins and a short triangular apex (Fig. 6A, B), while others have a more extensively tapering apex (Fig. 6D, E). Additionally, there are larger, narrow tapering leaves with stomata that are oriented parallel to the leaf axis (Fig. 6F). One leafy shoot has structures in the leaf axes that may be the broken stalks of pollen cones (Fig. 6A, B).

Conifer foliage type 3 is abundant at the Allon locality, and more than one taxon may be represented. In gross morphology some specimens of this leaf type are similar to *Taxodium wallisii* Aulenback & LePage (1998) from the Maastrichtian of Alberta. However, Aulenback and LePage (1998) noted that foliage of *Taxodium* Rich., *Cryptomeria* D. Don., and *Glyptostrobus* Endl. can be difficult to distinguish without associated reproductive material, and that material previously assigned to these genera from the Cretaceous and Tertiary is in need of re-evaluation. One difference between the isolated leaves from Allon (Fig. 6F) and *Taxodium wallisii* is that the stomata on the former are oriented parallel to the leaf axis, whereas they are randomly oriented in *Taxodium wallisii* (Aulenback & LePage, 1998). Some of the Allon conifer shoots (e.g., Fig. 6A, B, D) are broadly similar to specimens from the Late Cretaceous (late Santonian-early Campanian) of southern Sweden assigned to the fossil genus *Quasisequoia* Srinivasan & Friis (1989). Other specimens (e.g., Figs. 6E, F) more closely resemble specimens from southern Sweden assigned to *Elatidopsis* Srinivasan & Friis (1989).

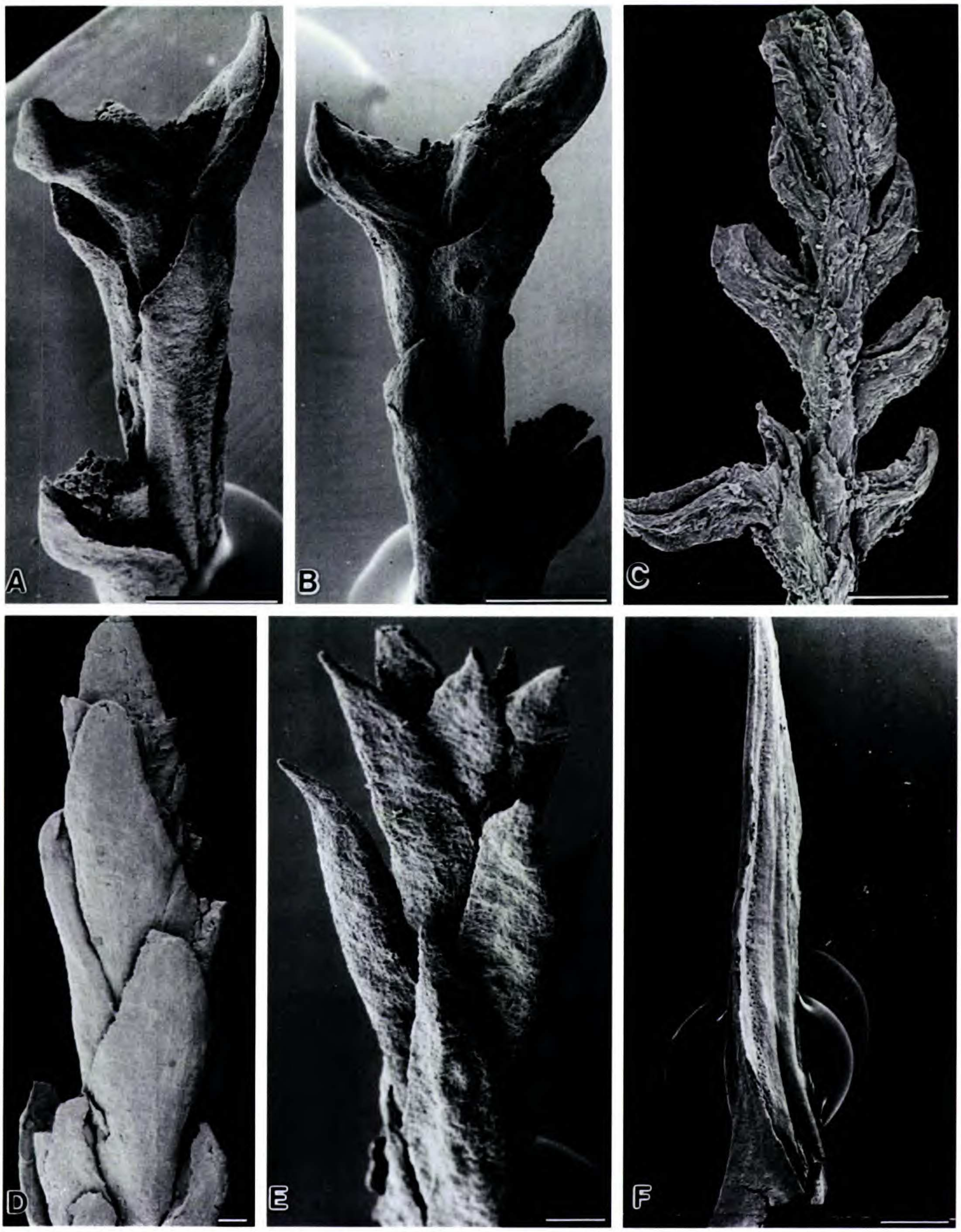


Figure 6. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 8, Conifer foliage type 3. —A. Conifer shoot with short, scale-like leaves with parallel margins, acute apex, and decurrent base showing possible cone stalk in leaf axil; PP45164. —B. Other surface of specimen shown in A. —C. Conifer shoot with short, thick, scale-like leaves with an acute apex and decurrent base; PP45165. —D. Conifer shoot with short, scale-like leaves with a tapering rounded apex and decurrent base; PP45166. —E. Conifer shoot with short, scale-like leaves with a tapering acute apex and decurrent base; PP45167. —F. Isolated conifer leaf with acute apex and two parallel lines of stomata on the adaxial surface; PP45168. Scale bars: A–C, F = 0.5 mm; D, E = 100 μm.

Both *Quasisequoia* and *Elatidopsis* are of probable taxodiaceous affinity.

Conifer family *incertae sedis*

9. Conifer foliage type 4 (cf. *Brachyphyllum*)
Figure 7.

Conifer shoot fragments with short, broadly triangular, tightly appressed helically arranged scale leaves (Fig. 7A–C). Leaves are 3–4 mm long, 2–3 mm wide. The abaxial epidermis bears numerous, longitudinally oriented, parallel rows of stomata (Fig. 7D). The leaves have thin fimbriate margins.

These specimens are common in the Allon mesofossil assemblage and may represent the mesofossil equivalent of taxon 6 (conifer foliage type 1 [cf. *Brachyphyllum*]), which is known as a macrofossil, but more detailed study is required based on additional material.

10. Conifer pollen cone and dispersed cone scales
Figure 8.

Conifer pollen cones bear helically arranged, imbricate cone scales (Fig. 8A, B). The cones are ca. 8 mm long, 5–6 mm wide. Cone scales have a narrow stalk proximally and a broad peltate limb with a fimbriate margin distally (Fig. 8C–E). Pollen grains are not preserved.

Epidermal details have not yet been studied to determine whether these cones were produced by the same plant species as one of the conifer foliage types, but the strongest morphological similarities are with the leaves of conifer foliage type 4 (cf. *Brachyphyllum*). The Allon pollen cone is similar to probable taxodiaceous pollen cones and sporophylls that were described from the Åsen locality in southern Sweden (Srinivasan & Friis, 1989, plate 8). Fragments of conifer cones are relatively common in the Allon flora, and more than one taxon may be represented.

ANGIOSPERMS

Magnoliales

11. cf. *Detrusandra* Crepet & Nixon
Figure 9.

Flowers ca. 5 mm tall, 3 mm wide, with numerous helically arranged perianth parts that are connate basally to form a deep floral cup (Fig. 9A, B). Stamens numerous, laminar, inserted on inner surface of cup; filament and anther are not differentiated. Carpels numerous, apparently spirally arranged, inserted in the base of the floral cup. Pollen unknown.

Crepet and Nixon (1994, 1998) described several types of fossil flowers with deep floral cups from the Turonian of New Jersey. They concluded that some of the flowers are most similar to the Eupomatiaceae (Magnoliales), and that others are more similar to the Calycanthaceae (Laurales). Cladistic analyses of relationships of two fossil taxa of magnoliid flowers showed that these taxa cannot be referred to any extant family (Crepet & Nixon, 1998). The flowers described here are most similar to the fossil *Detrusandra mystagoga* Crepet & Nixon (1998). Although similar to Calycanthaceae in many respects, these fossils differ from members of the extant family in the absence of elongated stigmas on the carpels and other features (Crepet & Nixon, 1998).

This taxon is represented in the Allon flora by three specimens.

Lauraceae

12. *Mauldinia* sp. Drinnan, Crane, Friis & Pedersen
Figure 10.

Flowers borne on flattened, bilobed inflorescence units, 6–7 mm wide, 5–6 mm long (Fig. 10A, B). Flowers trimerous with perianth in two cycles of three; the tepals of the outer cycle are shorter than those of the inner cycle. Details of androecium and pollen unknown. The gynoecium consists of a single carpel with a superior ovary.

Mauldinia was originally described by Drinnan et al. (1990) from an early Cenomanian locality in northern Maryland, and has since been found at other mid and Late Cretaceous localities in North America, Europe, and Asia (Drinnan et al., 1990; Eklund & Kvaček, 1998; Herendeen & Crane, unpublished data). The inflorescence structure of *Mauldinia* is unique and unlike that found in extant Lauraceae, but in those cases where flower structure is understood in detail it is consistent with extant members of the family (Drinnan et al., 1990; Eklund & Kvaček, 1998). The inflorescence of *Mauldinia* is spicate with helically arranged lateral cladode-like inflorescence units that are flattened, deeply bilobed, and typically bear five flowers and associated subtending bracts (Drinnan et al., 1990). The material described here is preserved as lignitized and compressed specimens, not as charcoal.

Wood of *Mauldinia mirabilis* Herendeen (*Paraphyllanthoxylon marylandense*) was described by Herendeen (1991a). *Paraphyllanthoxylon* is one of the most common types of angiosperm wood in the Late Cretaceous, and it is likely that much of it is referable to the Lauraceae (Herendeen, 1991a).

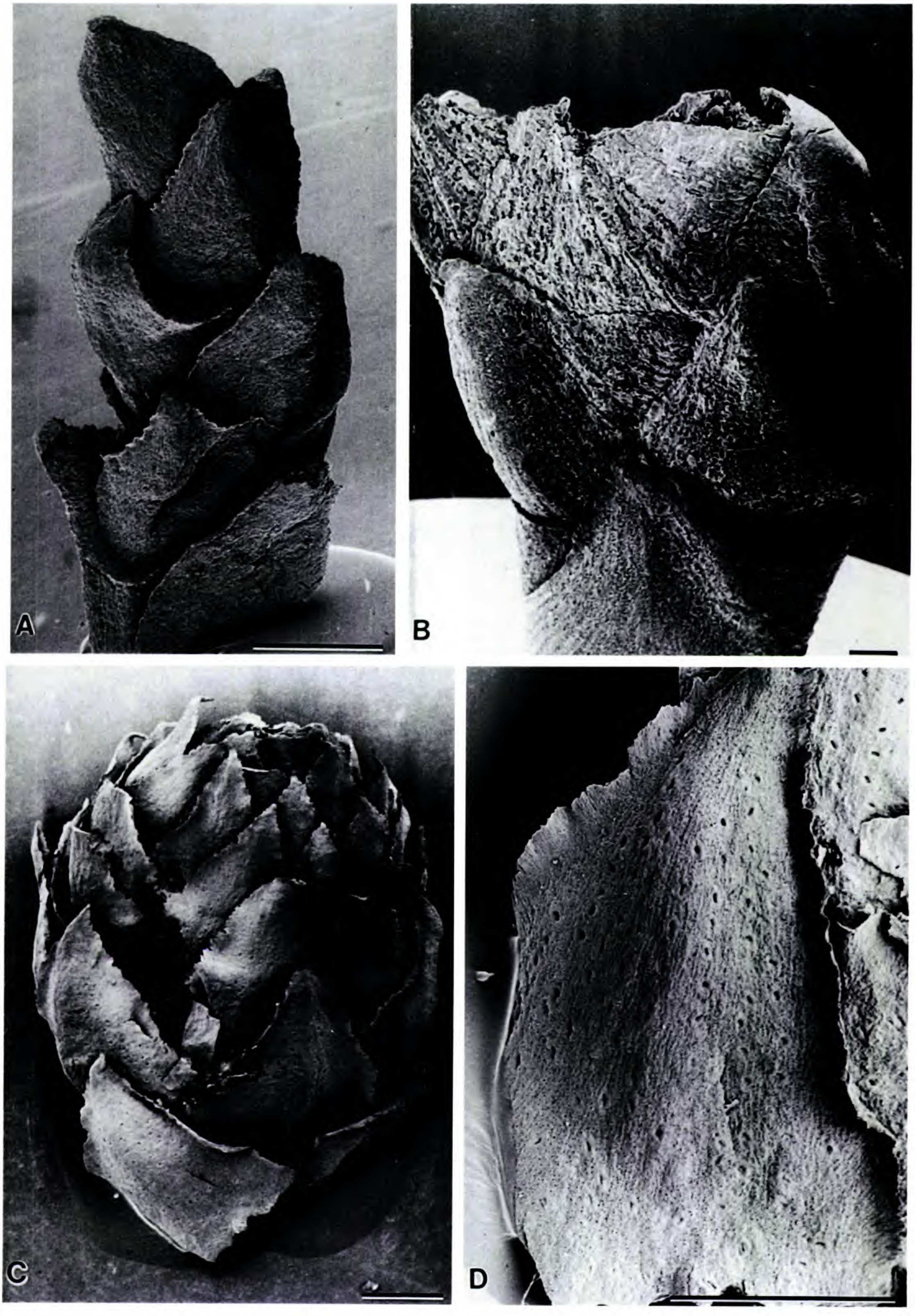


Figure 7. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 9, Conifer foliage type 4 (cf. *Brachyphyllum*). —A. Conifer shoot with short, broad scale-like leaves; note upturned acute apices (cf. Fig. 5B); PP45169. —B. Conifer shoot with short, broad scale-like leaves; PP45170. —C. Conifer shoot with short, broad

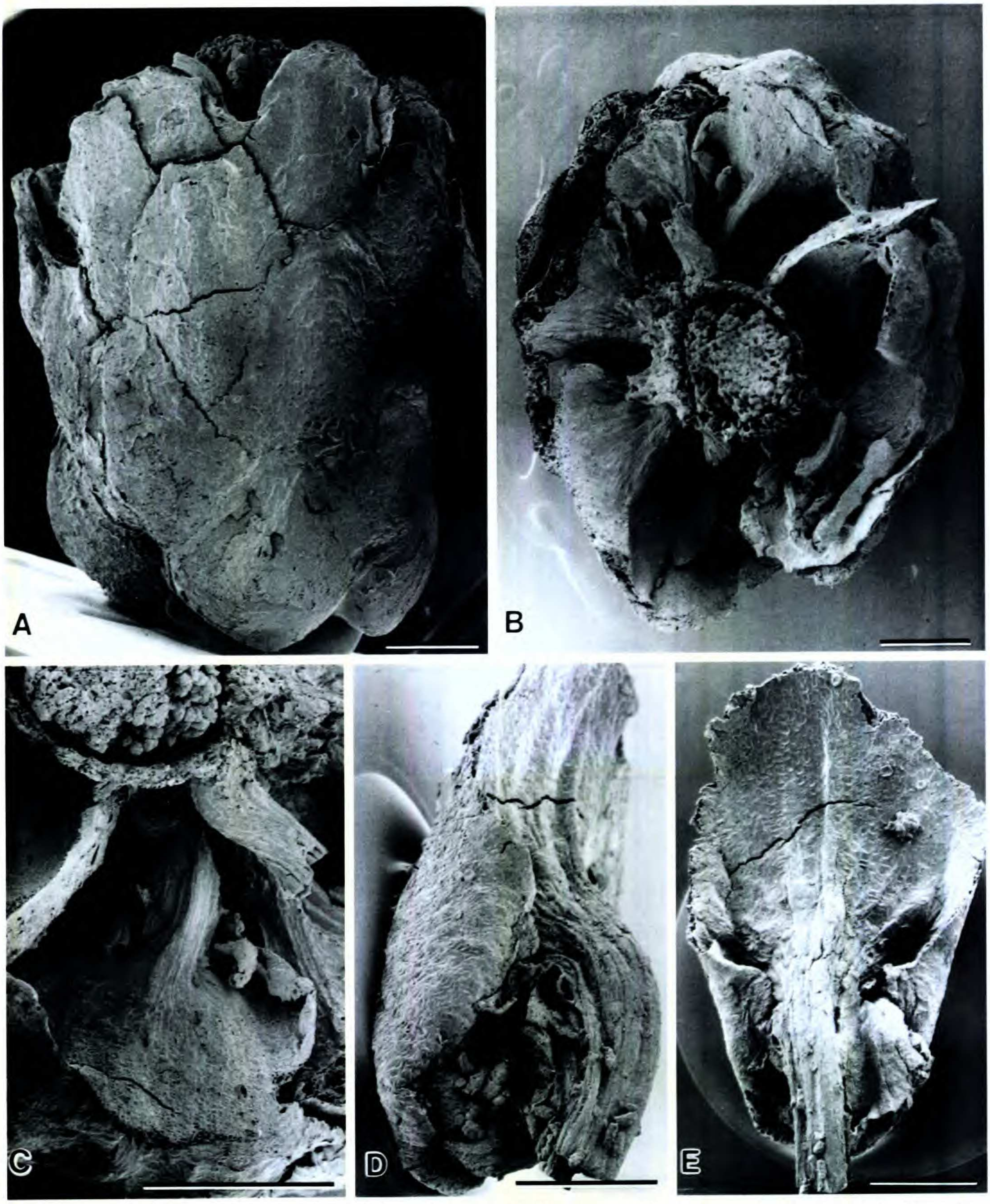


Figure 8. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 10, Conifer pollen cone and dispersed cone scales. —A. Lateral view of conifer pollen cone with imbricate cone scales; PP45172. —B. Apical view of conifer pollen cone in A. —C. Detail of pollen cone in A showing attachment of scale to axis. —D. Lateral view of isolated pollen cone scale; PP45173. —E. Cone scale in D viewed from inner (adaxial) surface. Scale bars: A–C = 1 mm; D, E = 0.5 mm.

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scale-like leaves; note stomata on adaxial surface; PP45171. —D. Detail of leaf from specimen in C showing detail of fimbriate leaf margin and abaxial surface with stomata. Scale bars = 0.5 mm.

Figure 9. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 11, cf. *Detrusandra* Crepet & Nixon (Magnoliales). —A. Lateral view of longitudinally fractured flower showing numerous tepals incurved at the apex and numerous carpels; PP45174. —B. Same specimen as A from opposite side; lateral view showing hypanthial cup bearing numerous free tepals incurved toward the apex and along the margin. Scale bars = 1 mm.

cf. Triuridaceae

13. Trimerous staminate flower
Figure 11.

Staminate flowers are actinomorphic with six perianth parts and three stamens. The perianth parts are basally united forming a zone ca. 0.1 mm wide. Distally the perianth parts are free, 0.8–1.0 mm long, 0.6–0.7 mm wide, and taper to a rounded apex. The androecium consists of three stamens in a single cycle. The stamens are united at the base. In some specimens the anthers are sessile in the center of the flower (Fig. 11A, D), while in others they are elevated on a thick, central column, which apparently results from fusion of the filaments (Fig. 11B, C). The anther connective is thick and extends beyond the anther sacs. Anthers dehisce longitudinally and are extrorse. Pollen is monosulcate. Pistillate flowers are unknown.

Flowers similar to the specimens from Allon were described by Gandolfo et al. (1997a, 1998b) from the Turonian of New Jersey as the oldest representatives of the achlorophyllous monocot family Triuridaceae. Gandolfo et al. (1997a) observed variation in tepal and connective morphology among their specimens and concluded that the fossils represent at least four species of related plants. The specimens from Allon also exhibit morphological variation, and one of the variants (with the anthers attached to the apex of a swollen column Fig. 11B, D) is apparently not represented among the suite of specimens from New Jersey (Gandolfo et al., 1997a, 1998b). This taxon is represented in the Allon assemblage by about five specimens.

Monocot, family *incertae sedis*

14. Tricarpellate flower
Figure 12.

Flowers trimerous, actinomorphic, apparently bisexual, ca. 0.7 mm diameter, 0.5–0.8 mm long; perianth abraded, apparently consisting of one cycle of three tepals (Fig. 12A, D); androecium incompletely preserved, only filament bases present, apparently consisting of two cycles of three stamens (Fig. 12C, D); pollen grains preserved on the fruit surfaces, monosulcate, exine reticulate, coarse near the middle of the grain and becoming finer toward the ends; polar axis 22 μm, equatorial axis 12 μm. The gynoecium consists of three free carpels; the

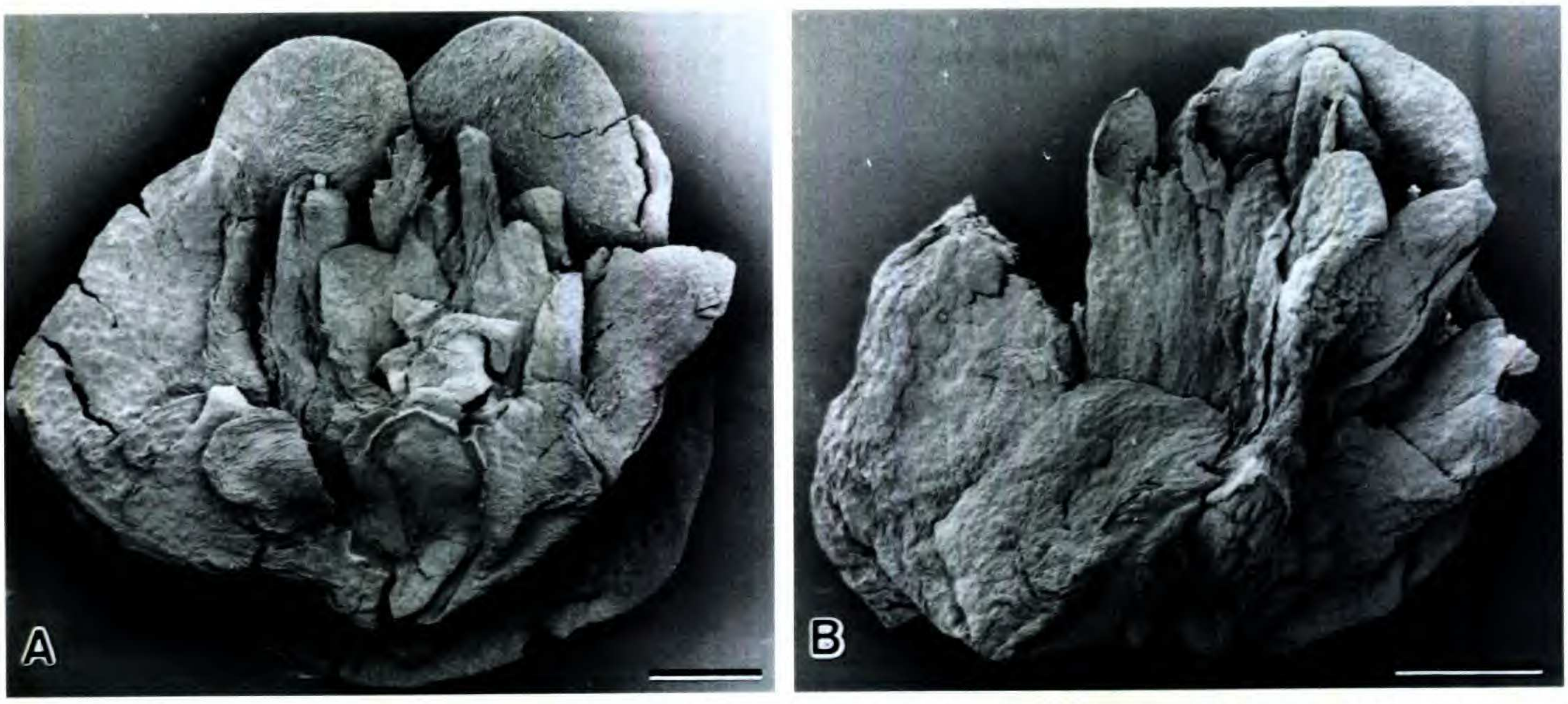


Figure 10. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 12, *Mauldinia* sp. Drinnan, Crane, Friis & Pedersen (Lauraceae). —A. Adaxial surface of flattened, bilobed inflorescence unit with several attached flowers; PP45175. —B. Adaxial surface of inflorescence unit showing tepals and other floral parts of several flowers; PP45153. Scale bars = 1 mm.

ovary is superior; styles are well differentiated and distinct, although confluent for most of their length (Fig. 12B).

Only two specimens of this fossil type are known. Both specimens, which are well-developed fruits, contain only abraded perianth remnants. The perianth and androecium are poorly understood. Additional material is required for detailed characterization. The monosulcate pollen associated with this taxon is similar to fossil pollen grains assigned to *Liliacidites* (Walker & Walker, 1984, 1986). Pollen grains of this type are similar to those of some monocotyledons (Doyle, 1973; Friis et al., 1999).

15. Monocot leaf type 1
Figure 13A.

Leaf fragments with very fine parallel venation (Fig. 13A). Maximum length ca. 200 mm (incomplete), maximum width ca. 70 mm (incomplete).

This leaf type is represented by two specimens. It differs from similar leaves grouped as monocot leaf type 2 (taxon 16) in its more fragile (less coriaceous) texture, its greater width and the absence of a thicker midrib region. Monocot leaf type 1 is similar in overall form to *Doryanthites cretacea* described by Berry (1914, pl. 17, fig. 3) from the Eutaw Formation (Santonian-Campanian) of Georgia, but additional details are needed to pursue this comparison further.

16. Monocot leaf type 2
Figure 13B.

Leaf fragments with fine parallel venation; apparently with parallel margins. Maximum length ca. 60 mm (incomplete). Maximum width ca. 16 mm. Center of the leaf occupied by a darker region perhaps indicating greater leaf thickness (Fig. 13B). It is unclear whether there is a single thick central vein or just a cluster of parallel veins embedded in thicker leaf tissue.

This leaf type is represented by a single specimen in our collections. While almost certainly a monocot, the systematic affinity of this leaf type within the group is uncertain. This specimen may ultimately be resolved as a variant of monocot leaf type 1.

Hamamelidaceae subfamily Hamamelidoideae

17. *Allonia decandra* Magallón-Puebla, Herendeen & Endress
Figure 14A–C.

Flowers actinomorphic, pentamerous, ca. 2.75 mm from base to tip of anthers. Perianth consists of a poorly preserved calyx represented by irregular, abraded lobes on the floral cup, and narrow, linear petals (apparently five in number). The androecium is composed of ten stamens in two alternating cycles of five (Fig. 14A). The stamens have a very short filament and a long anther with a well-developed extension of the connective (Fig. 14B). Pollen grains are spherical to slightly oblate, 21–26 μm in diameter, tricolpate with a prominent reticulum. Internal to the stamens are structures that may represent a nectariferous disk. The gynoecium is unknown. Isolated seeds similar to those of extant subfamily Hamamelidoideae also occur in the Allon flora (Fig. 14D, E). The seeds

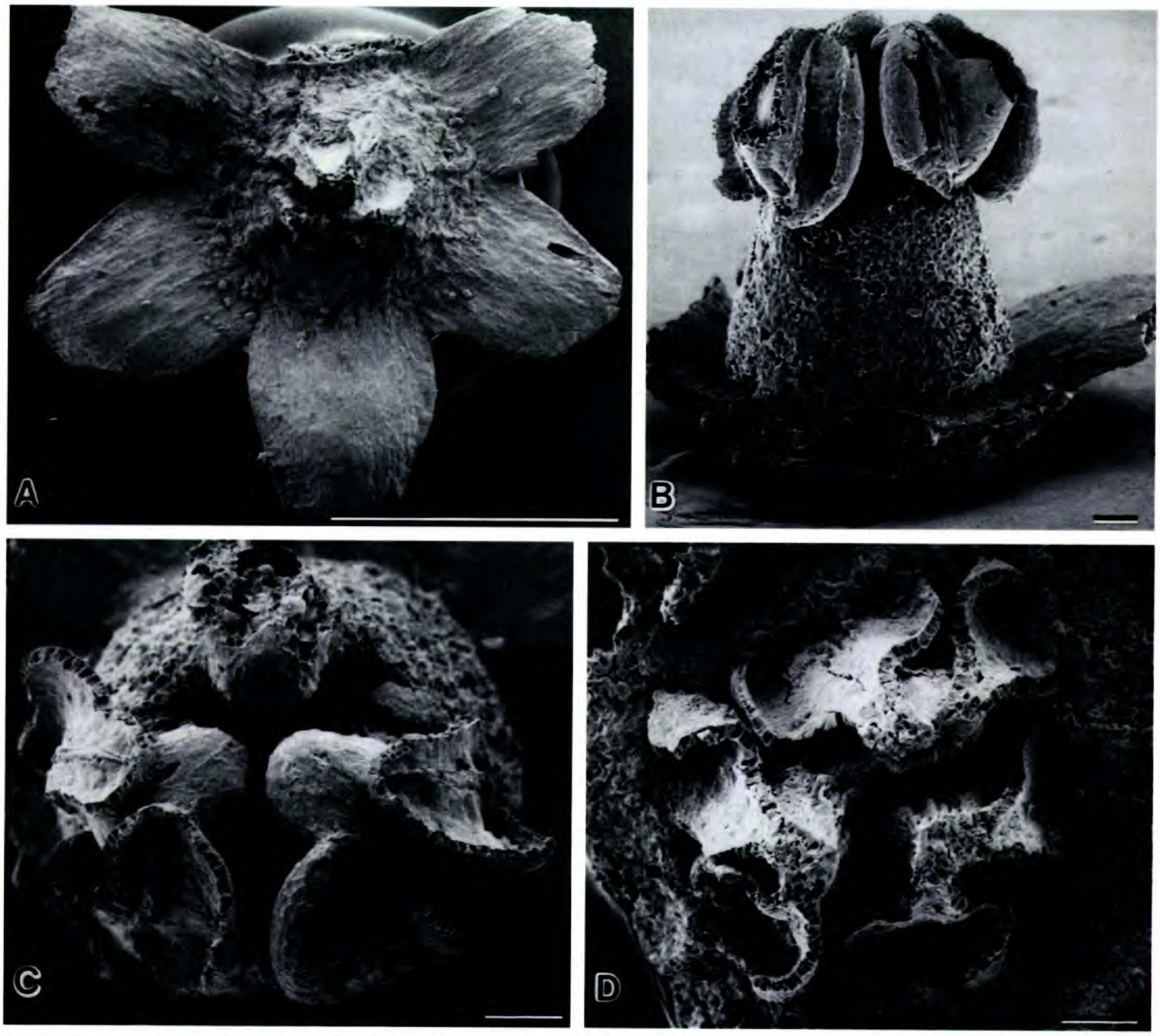


Figure 11. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 13, Trimerous staminate flowers (cf. Triuridaceae). —A. Staminate flower with six perianth parts (one broken at base) and three stamens with remains of open sessile anthers; PP45176. —B. Lateral view of staminate flower with three anthers borne on a central fleshy column; PP45177. —C. Apical view of stamens from B showing open thecae and fleshy apical extension of the connective; PP45177. —D. Detail of broken staminate flower with sessile extrorse anthers showing details of the anther wall in cross section; PP45178. Scale bars: A = 1 mm; B–D = 100 μm.

are 1.0–1.2 mm long, 0.25–0.36 mm wide, approximately oval in outline with an oblique, elongate hilum.

This fossil flower was described in detail by Magallón-Puebla et al. (1996). The morphological and palynological features observed in *Allonia* indicate an affinity to the subtribe Loropetalinae (tribe Hamamelideae). Cladistic analysis of the relationships within Hamamelideae placed *Allonia* as sister taxon to the extant southeast Asian genus *Maingaya* Oliver, which includes a single species. *Allonia* is represented in the Allon flora by one incomplete flower specimen and numerous dispersed anthers. Dispersed seeds number ca. 15.

cf. Hamamelidaceae

18. Flower with apically connate stamen connectives
Figure 15.

Flower small, ca. 1.5 mm in diameter, actinomorphic, hypogynous and 5-parted. The perianth is represented by five petals or their bases. The androecium is formed by ten stamens in two whorls of five. The stamens have a very massive filament (Fig. 15D, F), short anthers, and a long apical expansion of the connective. The filaments are laterally connate near their base, forming a proximal continuous androecial ring (Fig. 15A). The stamens

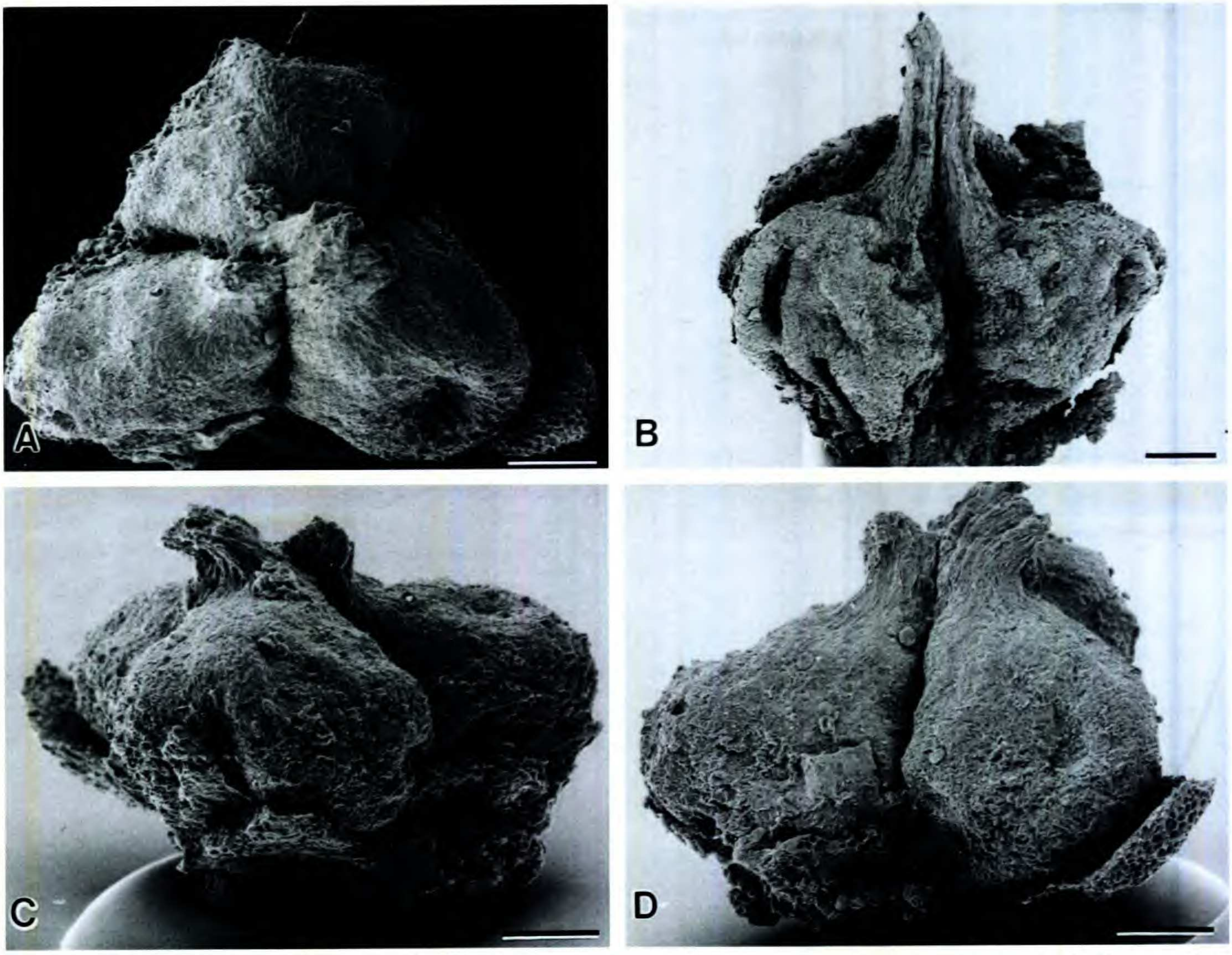


Figure 12. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 14, Tricarpellate flower (cf. monocots). —A. Apical view of trimerous flower showing tricarpellate gynoecium; PP45179. —B. Lateral view of young fruit showing elongated, separate but confluent, styles; PP45180. —C. Oblique view of specimen in A showing remains of perianth and filament bases. —D. Lateral view of specimen in A and C showing perianth part. Scale bars = 100 μm.

of the inner whorl have four pollen sacs, but the stamens of the outer whorl are bisporangiate. Abundant pollen grains are found on the adaxial surface of stamens and on the center of the flower. Pollen grains are tricolpate, with a coarse, slightly heterogeneous reticulate exine ornamentation. The details of structures in the center of the flower are currently uncertain.

This complex flower is known from only two specimens. The crowding of parts in the center of the flower, and the presumed modified condition of several floral organs have precluded a secure identification of the nature of the available structures, and the interpretation of floral organs. Therefore, the floral structure described here is currently tentative. Detailed examination and dissection of additional specimens will be necessary to fully understand the organization of this flower type. Based on the preliminary data currently available, the elongate apical extensions of the connective, the basically pentamerous architecture, and the exine sculpture of the pollen grains suggest a possible relationship to the subfamily Hamamelidoideae (Hamamelidaceae). However, further comparisons, including comparisons with other families of basal eudicots, are necessary once additional specimens are discovered.

cf. subfamily Altingioideae, Hamamelidaceae

19. Capitate inflorescence
Figure 16.

Inflorescence capitate, spherical, diameter 1.6 mm, flowers sessile (Fig. 16A, B). Material consists of a single, abraded specimen in fruit. The inflorescence bore at least 20 flowers. Perianth and androecium are unknown. The gynoecium consists of two united and at least partially inferior carpels. The styles are free. Each ovary has two locules and numerous ovules (Fig. 16C, D). Pollen unknown.

Only a single specimen of this taxon is available. The available character information is currently in-

Figure 13. Macrofossils for the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxa 15 and 16, Monocot leaves: light micrographs. —A. Taxon 15, Monocot leaf type 1, macrofossil; PP45379. —B. Taxon 16, Monocot leaf type 2, macrofossil; PP45380. Scale bars = 10 mm.

sufficient to assess systematic relationships, but the morphology of the inflorescence and fruits is suggestive of altingioid Hamamelidaceae. Additional specimens are needed to pursue this comparison further.

Fagaceae sensu lato

20. *Protofagacea allonensis* Herendeen, Crane & Drinnan
Figure 17.

Material consists of staminate inflorescence units, dispersed staminate flowers, fruits, and cupules. Staminate flowers are typically borne in seven-flowered dichasia subtended by three series of bracts (Fig. 17A). Flowers have six small imbricate tepals in two cycles of three, 12 stamens in two cycles of six, and a vestigial gynoecium with three styles surrounded by a mass of simple trichomes (Fig. 17B). Pollen is very small, prolate, tricolporate, and reticulate to microfoveolate. Associated fruits are triangular or lenticular in cross section and develop from epigynous flowers with two (Fig. 17D) or three (Fig. 17C) carpels. The triangular fruits bear six short tepals at the apex (Fig. 17C). Associated cupules are pedunculate, four-lobed, and bear three or more fruits (Fig. 17E). The cupule lobes bear three series of bracts similar to those subtending the staminate dichasia.

This fossil taxon was treated in detail by Herendeen et al. (1995). Comparisons of *Protofagacea allonensis* with extant taxa clearly indicate a relationship to extant Fagaceae sensu lato, based particularly on the presence of the cupule, the form of the fruits, and the morphology of staminate inflorescences and flowers. However, pollen morphology (probably plesiomorphic) differs from that of extant taxa. Detailed resolution of the affinities of *Protofagacea* will require a clearer understanding of characters and relationships among extant Fagaceae sensu stricto and Nothofagaceae. *Protofagacea allonensis* is one of the five most abundant angiosperm mesofossils in the Allon flora (> 1000 whole or partial specimens).

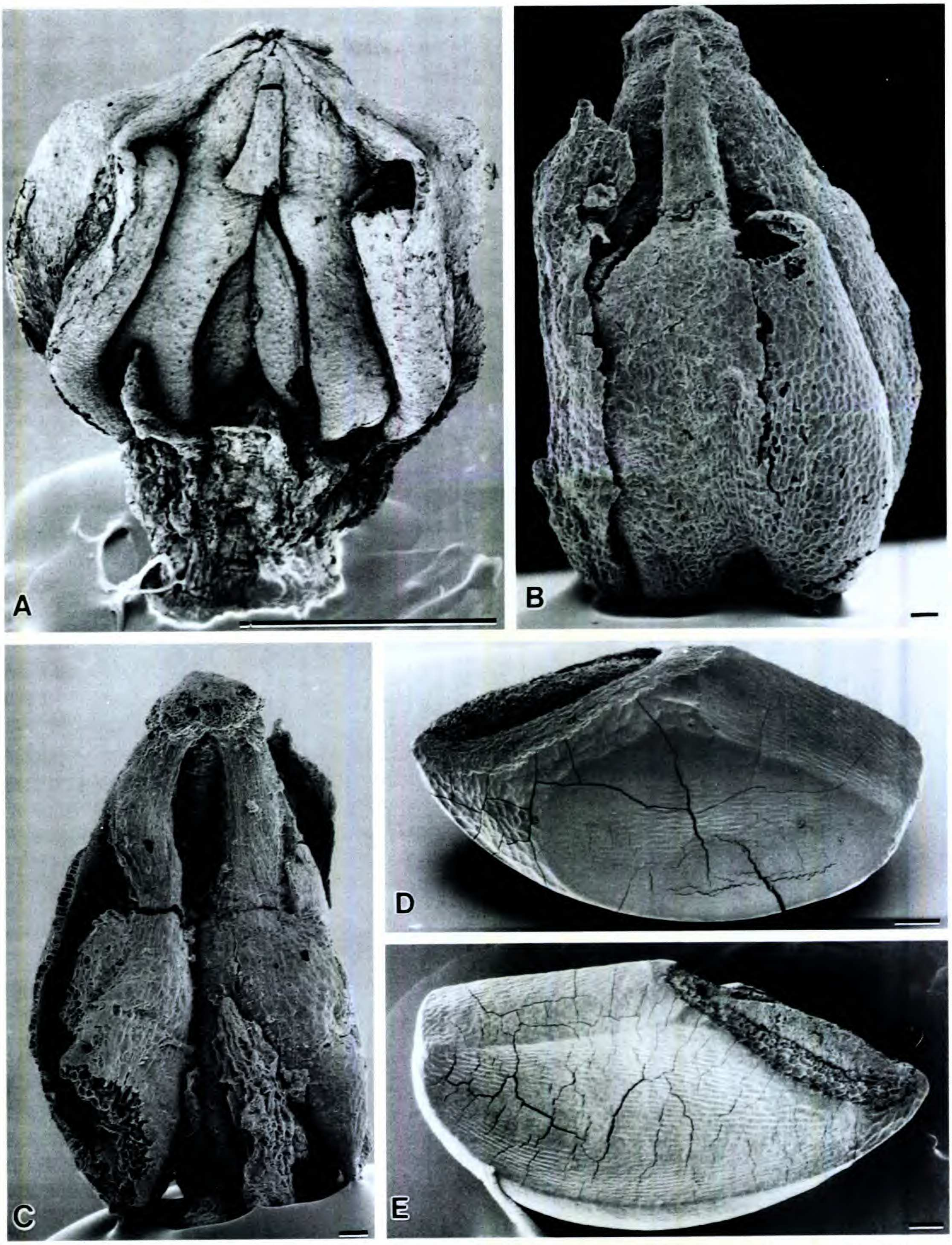
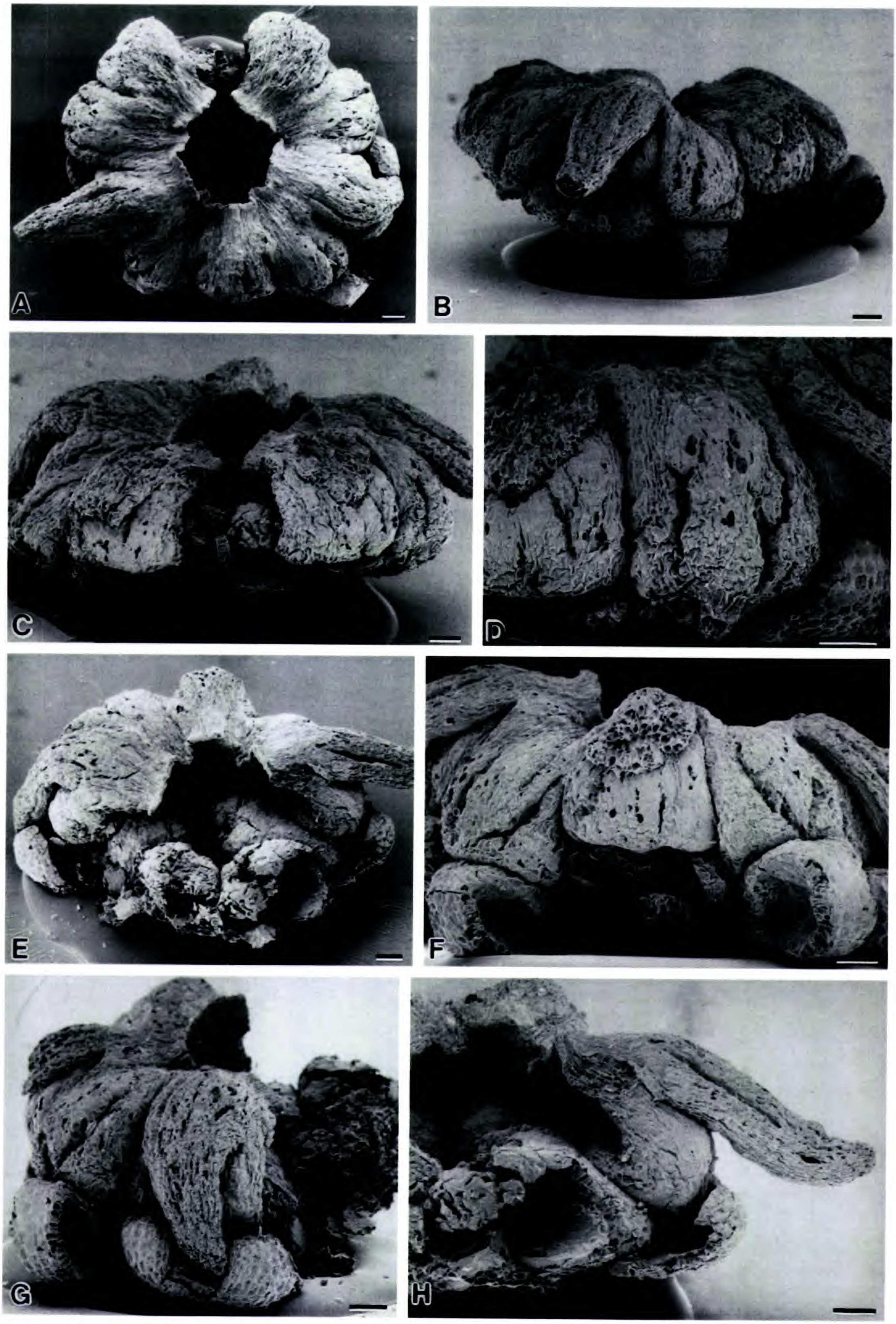


Figure 14. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 17, *Allonia decandra* Magallón-Puebla, Herendeen & Endress (A–C) and associated seeds (D, E) (Hamamelidaceae). —A. Oblique view of flower with ten stamens and sepal remnants; PP44595. —B. Abaxial view of stamen with long anther and a linear petal on the left; PP44676. —C. Adaxial view of specimen in B showing portions of two anthers and possible lobe of nectariferous disk. —D. Seed characteristic of Hamamelidoideae showing oblique elongate hilum scar; PP44685. —E. Seed characteristic of Hamamelidoideae showing oblique elongate hilum scar; PP44680. Scale bars: A = 1 mm; B–E = 100 μm.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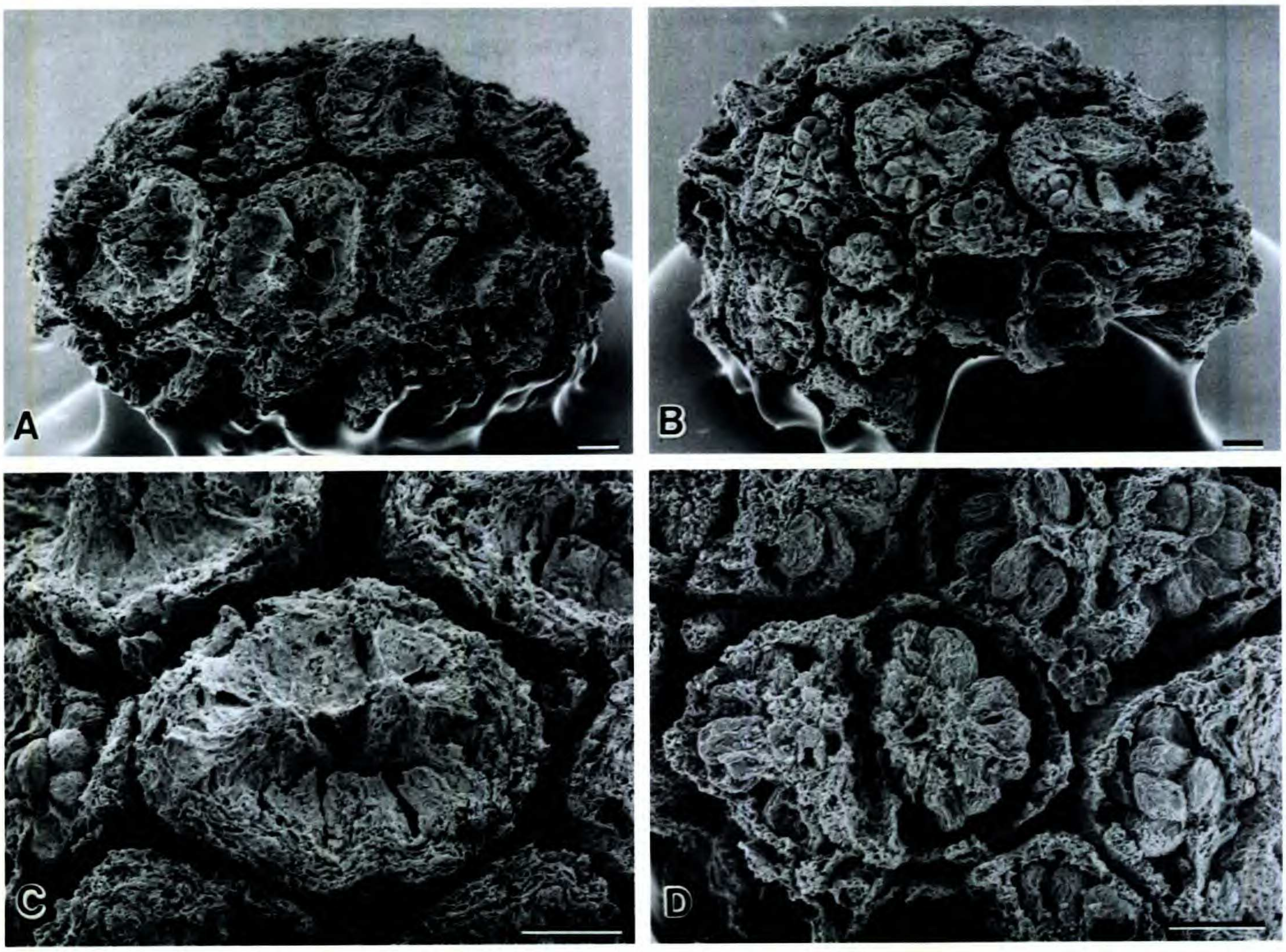

Figure 16. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 19, Capitate infructescence (cf. Hamamelidaeae subfamily Altingioideae). —A. Oblique view of infructescence showing arrangement of young fruits; PP45181. —B. Lateral view of specimen in A. Note the walls of some fruits are abraded, revealing numerous rounded ovules or seeds. —C. Apex of single fruit from infructescence in A, showing remains of two style bases. —D. Transverse section of fruit from infructescence in A, showing two locules and numerous rounded ovules or seeds. Scale bars = 100 μm.

21. *Antiquacupula sulcata* Sims, Herendeen & Crane

Figure 18.

Material consists of staminate flowers, bisexual flowers, fruits, and cupules. Staminate flowers are pedicellate (Fig. 18G), with six tepals in two cycles of three, 12 stamens, and a vestigial gynoecium with three styles (Fig. 18G–I). Bisexual flowers are epigynous and actinomorphic (Fig. 18D, E), with six free tepals in two whorls, 12 free stamens, and a syncarpous gynoecium with three styles that are partially connate below, with trichomes around and between the style bases. The ovary is trilocular with two anatropous, apically pendulous ovules per locule. Fruits are triangular in cross section, with nearly equal sides (Fig. 18C). Cupules contain at least six fruits (Fig. 18A, B). The staminate and bisexual flowers both have slender, thin-walled nec-

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Figure 15. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 18, Flower with apically connate stamen connectives (cf. Hamamelidaceae). —A. Apical view of flower, showing nine apically connate stamen connectives, with one empty space that probably corresponds to a stamen that has broken off; PP45232. —B. Lateral view of flower in A, showing pollen sacs and massive apical extensions of the stamen connectives. —C. Lateral view of flower, opposite side as in B, with empty space corresponding to a missing stamen. —D. Detail of extended stamen connective showing pollen sac below (right). —E. Oblique view of partially dissected flower showing broken pollen sacs and apical extension of the connectives. The center of the flower is comprised of a ring of bulbous structures (?nectaries). —F. Detail of stamens showing broken pollen sacs and prominent extensions of the connectives. —G. Detail of a stamen showing small pollen sacs and massive apical extension of the connective. —H. Lateral view of a stamen showing broken pollen sacs and apical extension of the connective. Scale bars = 100 μm.

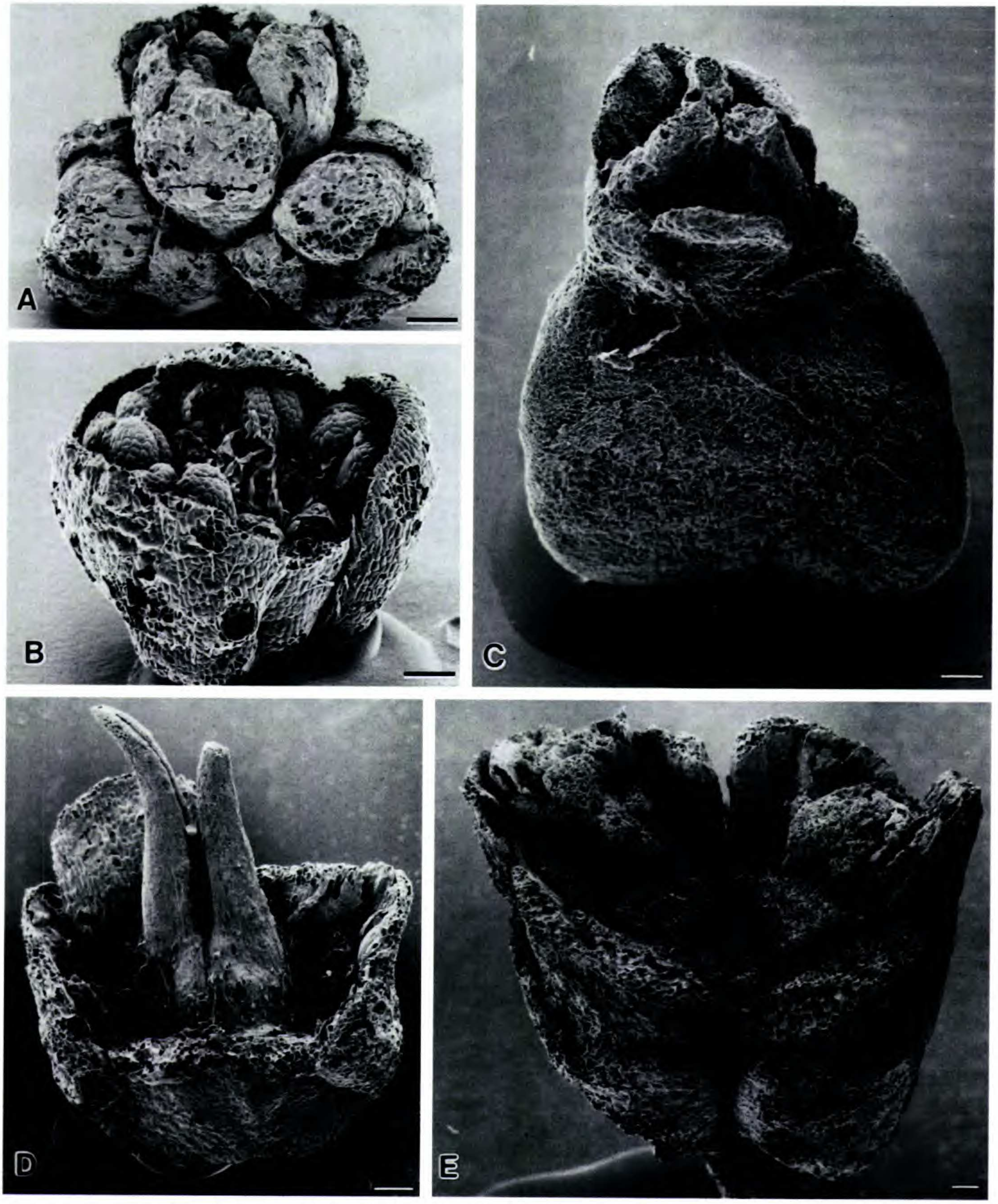

Figure 17. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 20, *Protofagacea allonesis* Herendeen, Crane & Drinnan (Fagaceae sensu lato). —A. Dichasium of trimerous staminate flowers; PP44457. —B. Single staminate flower showing anthers removed from dichasium; PP43838. —C. Tricarpellate fruit with epigynous perianth and three style bases; PP445777. —D. Small bicarpellate fruit showing remains of tepals; PP45183. —E. Cupule specimen showing fruit scars; PP44567. Scale bars = 100 μm.

tary lobes between the filament bases (Fig. 18I), and distinctive, multicellular glandular structures on the surface of the gynoecium. Pollen grains found in situ, and also on the surface of the flowers and fruits, are small and tricolporate, with a finely perforate tectum.

This fossil taxon was described in detail by Sims et al. (1998). *Antiquacupula* (and *Protofagacea*) shares several characters with extant rosids and hamamelids, and may prove to be a key taxon in future work examining relationships among these groups, as well as within the Fagaceae. The presence of a cupule, which is widely considered a synapomorphy of the family, plus trimerous flowers, and an inferior, trilocular ovary with two apically attached, pendulous, anatropous ovules per locule, are all characters of extant Fagaceae sensu lato, and support the relationship of *Antiquacupula* to this group. Current data are insufficient for confident assignment to a particular taxon within Fagaceae sensu lato.

Antiquacupula and *Protofagacea* share characters with both Nothofagaceae and Fagaceae sensu stricto, as well as with some families of Rosidae. Evaluating the relationships of *Antiquacupula* and *Protofagacea* is complicated by uncertainties regarding the relationships among extant Fagaceae. Recent cladistic analyses of morphological and/or molecular data have shown the Fagaceae sensu lato to be paraphyletic, and have therefore placed *Nothofagus* in a separate family from Fagaceae sensu stricto (Nixon, 1989; Chase et al., 1993; Manos et al., 1993; Manos & Steele, 1997). Under this interpretation, the presence of a cupule is no longer an unambiguous synapomorphy for the group. In this context, the presence of a cupule in the fossil taxon may support a relationship to the fagaceous grade, but it does not help to resolve relationships with respect to Fagaceae sensu stricto and Nothofagaceae. *Antiquacupula sulcata* is one of the five most abundant angiosperm mesofossils in the Allon assemblage (> 1000 whole or partial specimens).

cf. Juglandales/Myricales (family *incertae sedis*)

22. *Caryanthus* sp. Friis
Figure 19.

Flowers small, 1.1 mm long, 0.75 mm wide, apparently bisexual; epigynous (Fig. 19A, B), tepals free, imbricate; stamens six, free. Associated dispersed anthers are basifixed with longitudinal dehiscence slits. Pollen grains in situ within dispersed anthers, and on the surface of the flowers, are triaperturate with three very short colpi. Gynoecium composed of an inferior ovary (Fig. 19A–C) and a single style, locule number unknown; simple trichomes are present on the outer surface of the fruit wall. Pollen associated with these specimens is referable to the Normapolles pollen taxon *Pseudoplicapollis endocuspis* Tschudy (1975: 22, pl. 13, figs. 1–7, text-fig. 20).

A detailed treatment of this taxon is presented by Sims et al. (1999). Normapolles-type pollen grains are diverse and abundant in Late Cretaceous floras from eastern North America and Europe, but so far flowers with in situ Normapolles pollen have only been recovered from Europe (Friis, 1983; Friis & Crane, 1989) and the Allon locality (Sims et al., 1999). *Caryanthus knoblochii* Friis (1983), with which the Allon material shares many significant features, is probably closely related to extant Juglandales/Myricales. The species is represented in the Allon flora by five specimens.

23. Normapolles flower type A.
Figure 20.

The single known specimen is bisexual (designated as "Unnamed Normapolles flower A" by Sims et al., 1999), approximately 1.7 mm long, strongly flattened, and 1.1 mm in maximum width. The perianth and the androecium are poorly preserved (Fig. 20A, B). Apparently three stamen filaments are present, each opposite a tepal (Fig. 20C). Although none of the stamens are preserved with attached anthers, the filaments are covered with more than 30 grains of a single type of palynomorph. Pollen grains are triporate and small (ca. 10–11 μm in equatorial diameter), with a verrucate tectum. The ovary is inferior, style number is unclear. Although it is not possible to refer the pollen to a Normapolles pollen taxon without more data on internal structure, the grains appear to show polar thinning of the exine and circular external apertures, features exhibited by the post-Normapolles genus *Momipites*. The structural similarities of this flower to the Normapolles flowers described by Friis (1983) and the presence of probable *Momipites* pollen (Nichols & Ott, 1978; Frederiksen & Christopher, 1978) are both suggestive of a relationship to the Juglandales/Myricales.

cf. Betulaceae

24. *Bedellia pusilla* Sims, Herendeen, Lupia, Christopher & Crane
Figure 21.

Staminate flowers are actinomorphic, ca. 0.25–0.4 mm in diameter. Tepals free, imbricate, in two cycles of five, ca. 0.5–1.0 mm long, 0.1–0.2 mm maximum width (Fig. 21A–C). Stamens ten, free, filaments long, extending beyond tepals (Fig. 21C). Anthers ca. 0.6–0.9 mm long, basifixed, dehiscing by longitudinal slits (Fig. 21D). Ovary absent. Pollen grains oblate to peroblate, equatorial outline triangular with concave to occasionally straight sides and rounded corners. Pollen triaperturate with three very short colpi, weakly developed arci on


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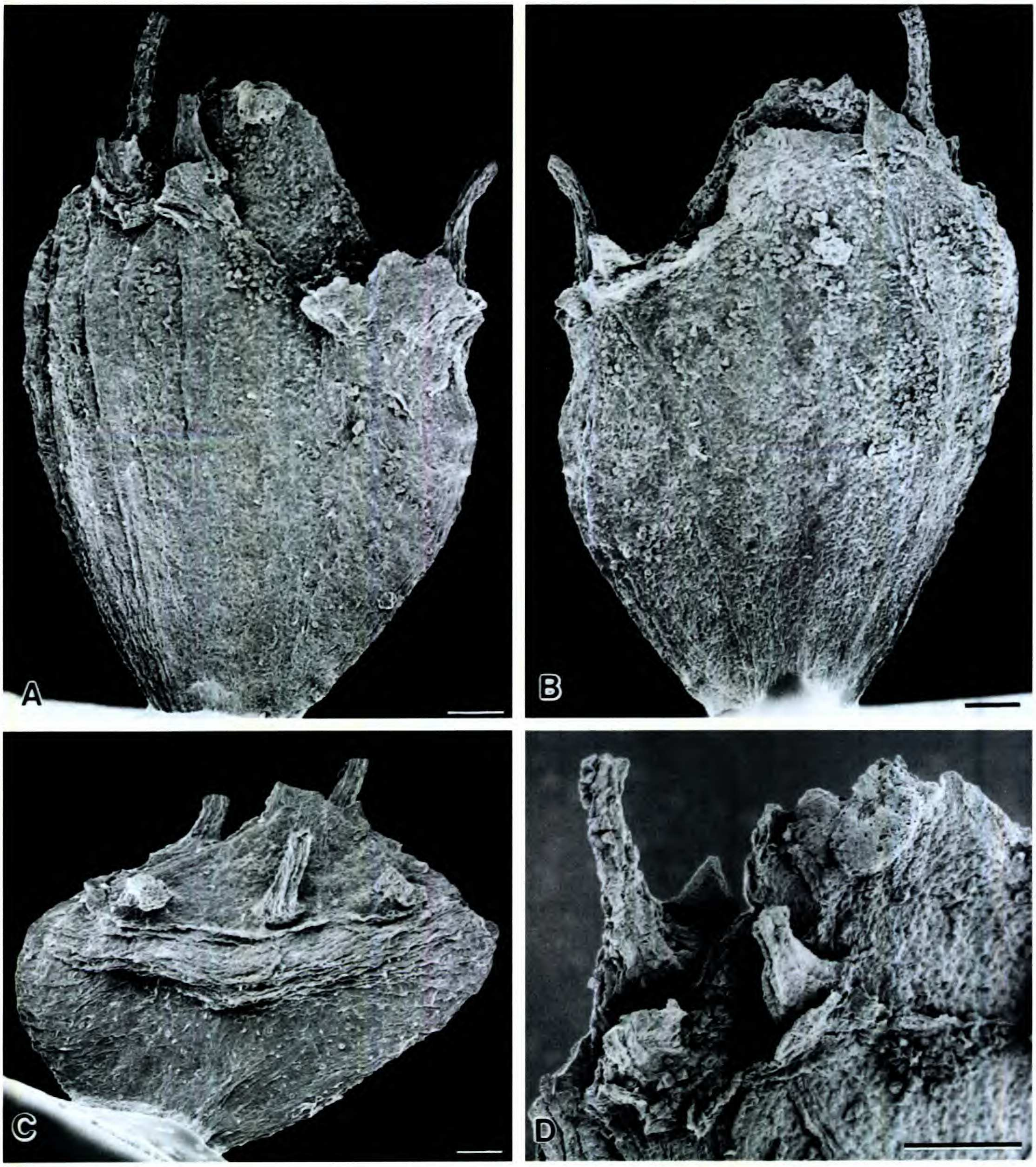

Figure 19. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 22, *Caryanthus* sp. Friis (cf. Juglandales/Myricales). —A. Lateral view of flower with remains of perianth and stamen filaments; PP45095. —B. Opposite side of flower shown in A. —C. Flower with remains of stamen filaments and single style; PP45096. —D. Oblique view of apex of flower in A showing numerous pollen grains around filament bases. Scale bars = 100 μm.

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Figure 18. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 21, *Antiquacupula sulcata* Sims, Herendeen & Crane (Fagaceae sensu lato). —A. Lateral view of cupule with young fruits; PP44751. —B. Apical view of cupule with fruits shown in A. —C. Incomplete cupule with one fruit; PP44752. —D. Lateral view of young fruit with attached perianth parts and stamen filaments; PP44764. —E. Apical view of fruit shown in D. —F. Lateral view of mature fruit showing longitudinal ribbing; note abraded perianth at apex; PP44814. —G. Lateral view of pedicellate staminate flower; PP44771. —H. Apical view of young staminate flower showing stamens and pistillode; PP44768. —I. Apical view of mature staminate flower; note filament bases alternating with presumed nectary lobes; PP44769. Scale bars: A–F, I = 1 mm; G, H = 100 μm.

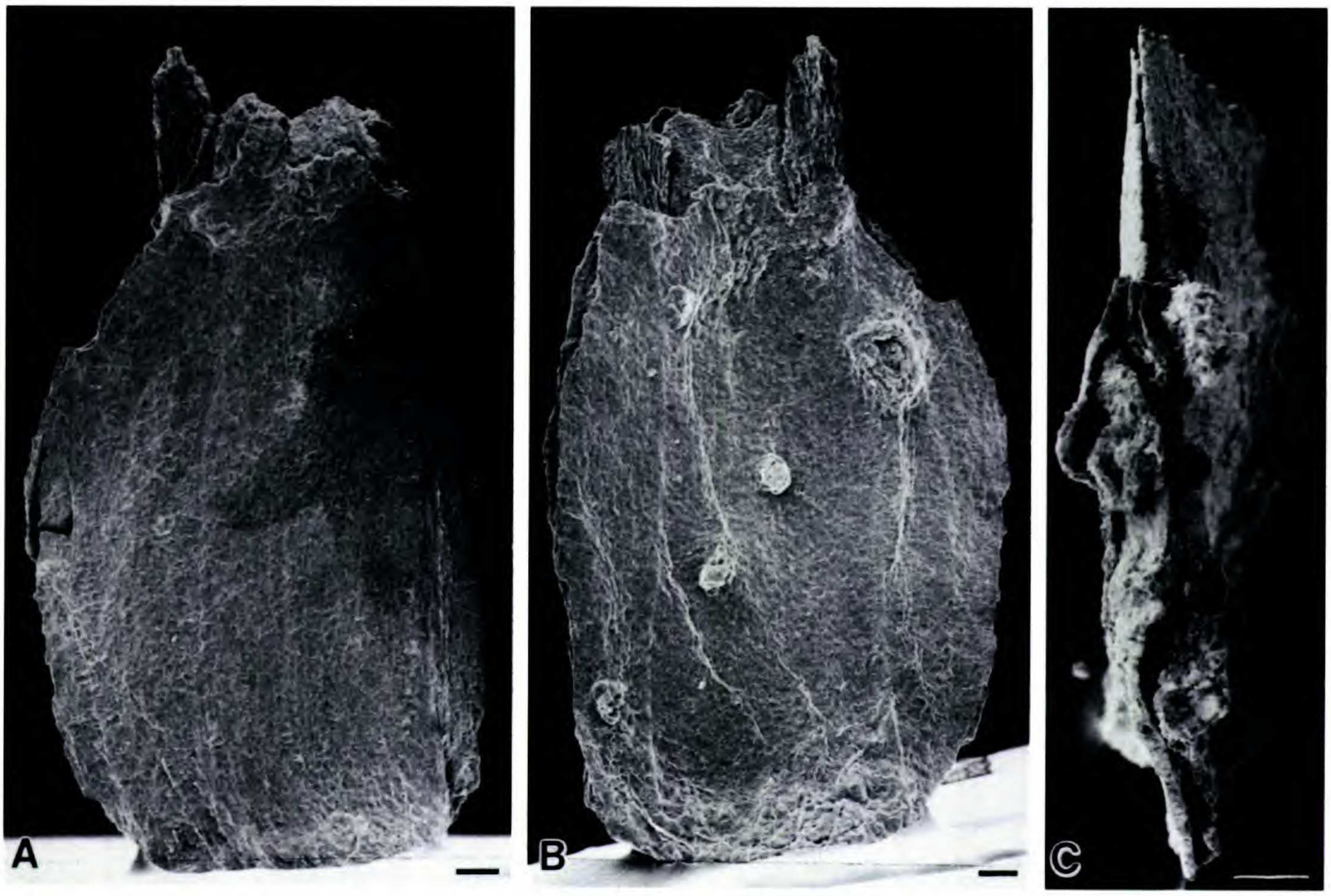


Figure 20. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 23, Normapolles flower type A (cf. Juglandales/Myricales). —A. Poorly preserved fruit with remains of perianth and stamen filaments; PP45097. —B. Opposite side of fruit shown in A. —C. Apical view of fruit shown in A and B. Scale bars = 100 μm.

each hemisphere and between apertural regions. Pistillate flowers and fruits are unknown.

The pollen associated with these specimens is referable to the Normapolles pollen taxa "New Genus D sp. D and New Genus D sp. A" of Christopher (1979), which were initially separated as two putatively distinct forms. The presence of arci (although weakly developed) and pollen ornamentation both suggest a relationship to Betulaceae. Some species of *Alnus* also have basically pentamerous flowers, although no extant Betulaceae have staminate flowers bearing ten perianth parts. *Bedellia* is represented in the Allon flora by four specimens.

Actinidiaceae

25. *Parasaurauia allonensis* Keller, Herendeen & Crane
Figure 22.

Flowers are actinomorphic, 0.7–1.2 mm long, 0.6–0.8 mm wide. Calyx composed of five imbricate sepals with multicellular trichomes on the abaxial surface (Fig. 22A). Corolla composed of five imbricate petals (Fig. 22B). Androecium of ten stamens, five of which are large, with the other five smaller, arranged in an alternating pattern (Fig. 22C, D). Anthers basifixed and deeply sagittate (Fig. 22C, D); pollen unknown. Gynoecium tricarpellate, with a syncarpous, superior ovary and three free styles emerging from an apical depression (Fig. 22E). The ovary is trilocular with intruded axile placentae bearing numerous ovules (Fig. 22F); mature fruit structure unknown.

The structure, phylogenetic relationships, and evolutionary significance of *Parasaurauia allonensis* were treated in detail by Keller et al. (1996). The fossil flowers and fruits are most similar to those of the family Actinidiaceae, which includes three extant genera, *Clematoclethra* (Franchet) Maxim., *Actinidia* Lindley, and *Saurauia* Willd. (Keller et al., 1996). Of these, *Parasaurauia allonensis* is most similar to *Saurauia*, differing only in the number of stamens (10 in the fossil vs. 15 to numerous in *Saurauia*). Like *Parasaurauia allonensis*, *Saurauia* has free styles with an adaxial longitudinal groove, simple stigmas, and three to five carpels. *Actinidia* has numerous stamens, frequently up to 30 carpels, and free styles with capitulate stigmas. Flowers of *Parasaurauia* are similar to Clethraceae and Diapensiaceae in being consistently tricarpellate, and are like most members of

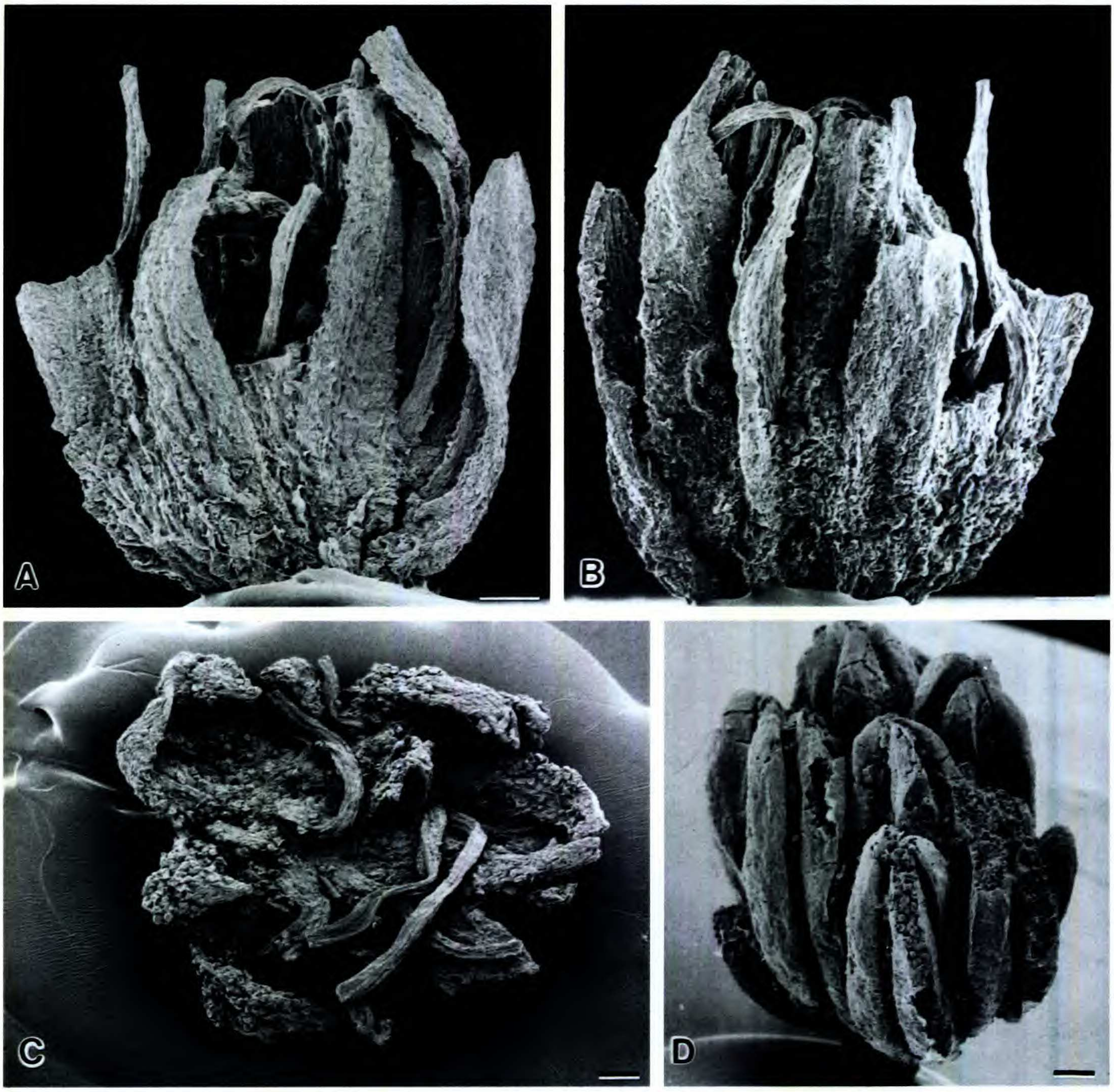


Figure 21. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 24, *Bedellia pusilla* Sims, Herendeen, Lupia, Christopher & Crane (cf. Betulaceae). —A. Staminate flower with well-developed perianth and stamen filaments; PP45099. —B. Opposite side of flower in A showing two whorls of perianth parts. —C. Apical view of compressed staminate flower showing perianth and stamen filaments with abundant adhering pollen; PP45100. —D. Lateral view of young staminate flower showing anthers and in situ pollen grains; PP45101. Scale bars = 100 μm.

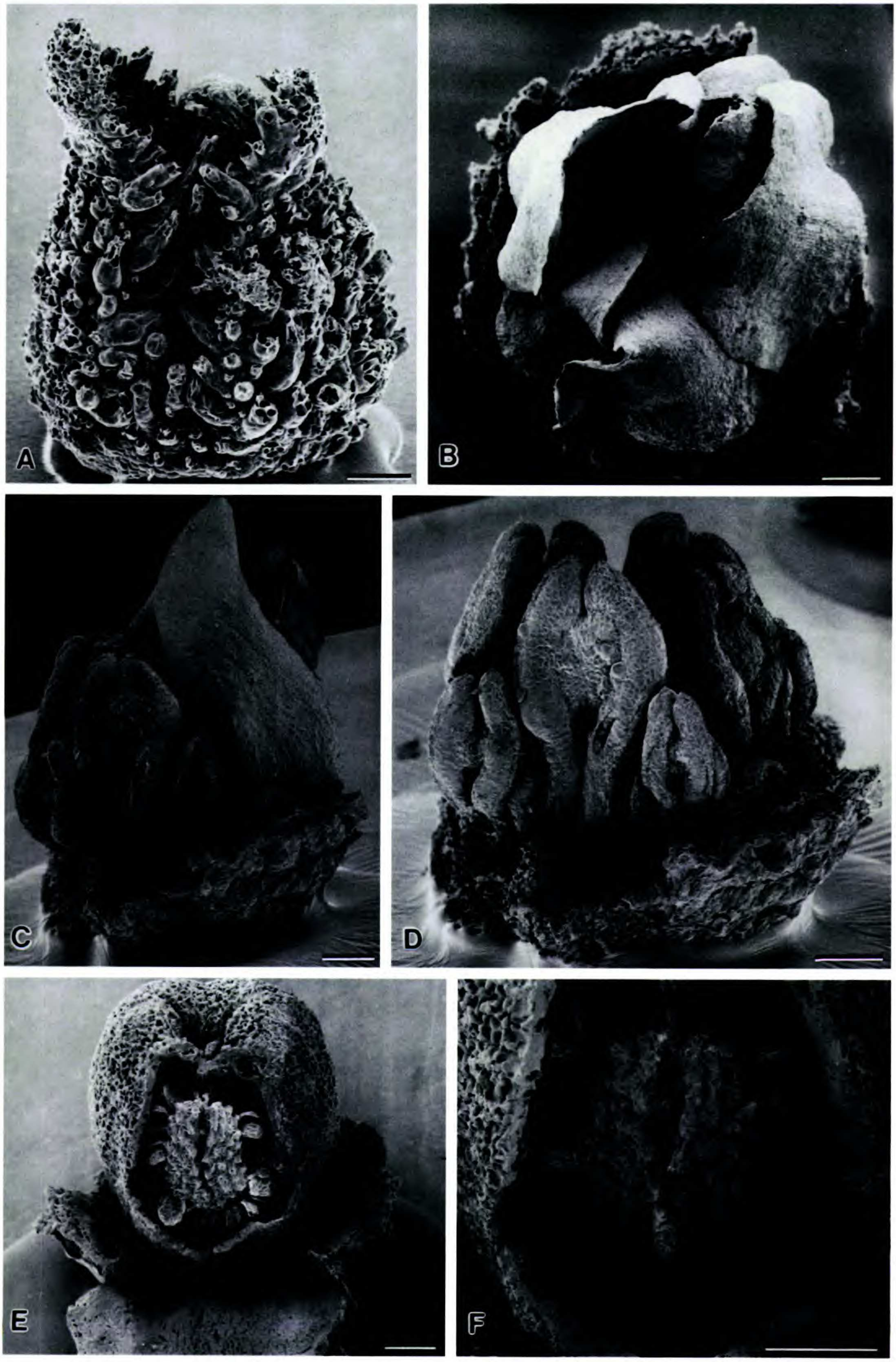
the Ericales in bearing 10 stamens. However, *Parasaurauia* differs most conspicuously from Clethraceae, Diapensiaceae, and other Ericales in having free styles.

Phylogenetic relationships of *Parasaurauia* were evaluated through a cladistic analysis (Keller et al., 1996). *Parasaurauia* is placed within the Actinidiaceae as sister to *Actinidia* plus *Saurauia*. *Clematoclethra* is resolved as the basal genus in the family. In this configuration, the free styles of *Parasaurauia*, *Actinidia*, and *Saurauia* are best interpreted as a synapomorphy that unites these genera, rather than a retained plesiomorphy in this group. Similarly, within the Actinidiaceae the presence of numerous stamens is a synapomorphy uniting *Actinidia* and *Saurauia* rather than a retained plesiomorphy.

cf. Ericales

26. Flower with stellate trichomes, type 1.
Figure 23.

Flowers are bisexual, hypogynous, actinomorphic, and pentamerous, ca. 3 mm long, 2 mm wide (Fig. 23A, B). The five sepals are free to the base, taper gradually to an acute apex, and apparently have only sparse stellate trichomes on their abaxial surface. The corolla is represented only by the ba-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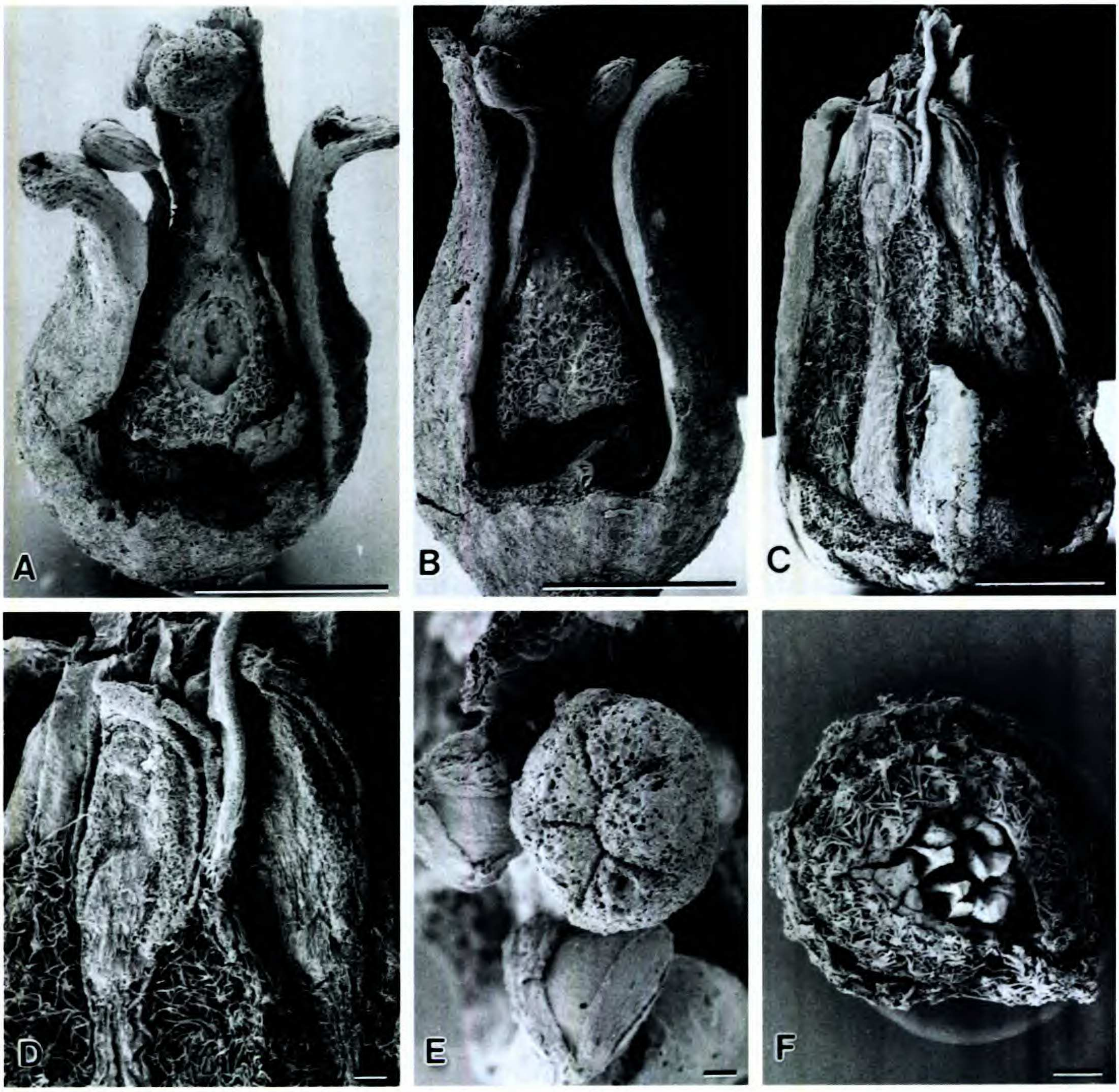

Figure 23. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 26, Flower with stellate trichomes, type 1 (cf. Ericales). —A. Oblique view of flower with valvate sepals, showing stellate trichomes and capitate stigma; PP45184. —B. Lateral view of specimen in A showing stamens with basifixed anthers and numerous stellate trichomes on ovary. —C. Specimen with sepals removed showing base of clawed petal, stamens, and numerous stellate trichomes; PP45185. —D. Detail of basifixed anther from specimen shown in C. —E. Capitate stigma with five lobes; PP45184. —F. Fruit with numerous stellate trichomes on fruit wall. Apex of fruit is broken showing tips of the internal septae; PP45186. Scale bars. A–C = 1 mm; D–F = 100 μm.

ses of clawed petals (Fig. 23C). The androecium consists of five free stamens with tangentially flattened filaments and basifixed anthers (Fig. 23D, E). Alternating with the stamen bases are five short, broad nectary lobes. The gynoecium consists of five connate carpels with a single style and a five-lobed, capitate stigma (Fig. 23E). Ovary locule number is unknown. The surface of the gynoecium and the

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Figure 22. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 25, *Parasaurauia allonensis* Keller, Herendeen & Crane (Actinidiaceae). —A. Flower bud showing sepals with conspicuous multicellular trichomes; PP44609. —B. Flower with sepals removed showing five imbricate petals; PP44612. —C. Lateral view of flower in B with three petals removed showing stamens with sagittate anthers. —D. Lateral view of flower shown in B, C with all petals removed. Note sagittate anthers and free styles in the center. —E. Fruit with locule broken open showing placentae and numerous seeds; PP44476. —F. Detail of specimen in E showing seeds. Scale bars = 100 μm.

filaments are covered by numerous stellate trichomes (Fig. 23F).

Fossil flowers very similar to these specimens from Allon were first described from the Campanian of Martha's Vineyard, Massachusetts (Tiffney, 1977). They are also known from the Turonian of New Jersey (Crepet, 1996, plate IV, 1–9; Crepet & Nixon, 1996, fig. 11A–G). The same flower is also known from fossil localities of similar age on Upatoi Creek in western Georgia (Herendeen et al., unpublished data). Flowers of this type are rare at the Allon locality.

27. Flower with stellate trichomes, type 2. Figure 24.

Flowers are bisexual, hypogynous, actinomorphic, 3 mm long, 2.5 mm wide, with pentamerous calyx, corolla, and androecium; number of carpels unknown. The five sepals are imbricate and free (Fig. 24B), with obtuse to acute apices. Numerous stellate trichomes cover the abaxial surface of the sepals (Fig. 24A). The corolla is represented only by the bases of clawed petals. The androecium apparently consists of five free stamens; filaments are not markedly flattened; anthers are unknown. Alternating with the stamen bases are five short, broad structures that we infer to be nectary lobes (Fig. 24D). The gynoecium consists of a syncarpous ovary with a single style (Fig. 24C); stigmas are not preserved. Ovary locule number is unknown. The ovary is roughly triangular in outline with rounded corners. The surface of the gynoecium, the filaments, and abaxial surface of the calyx also are covered by numerous stellate trichomes.

This fossil flower is similar in general organization to the previous taxon (taxon 26), except that the sepals are broader and are densely covered by stellate trichomes, the filaments are less strongly flattened, and the ovary is broader, shallower, and has a triangular outline. This taxon and the previous one may be variants of a single species or two species in the same genus. Similar variation was observed among the comparable fossils that were recorded from the Turonian of New Jersey (Crepet, 1996; Crepet & Nixon, 1996). Flowers of this type are very rare at the Allon locality.

28. Fruits bearing large peltate trichomes Figure 25.

Flowers bisexual, hypogynous, somewhat bilaterally symmetrical, ca. 3 mm long, 2 mm wide. Calyx composed of five thick, triangular, valvate sepals, three of which are broader than the other two (Fig. 25A, B). Corolla not preserved. Androecium composed of eight stamens, which alternate with eight square-shaped structures that we interpret as nectary lobes. The gynoecium consists of a superior ovary that is roughly triangular in outline, with a single style that appears to have a hollow, fluted central canal, and a stigma that is three-lobed. Internally, the ovary has three locules and massive axile placentae bearing numerous ovules (Fig. 25C). The fruit is a loculicidally dehiscent capsule (Fig. 25D). The abaxial surface of the sepals and the gynoecium are covered by numerous, overlapping, peltate trichomes.

Flowers identical to these have been reported from the Turonian of New Jersey (Weeks et al., 1996) and are also known from the Coniacian-Santonian of Georgia (Upatoi Creek; Herendeen & Crane, unpublished data). Weeks et al. (1996) used a cladistic analysis to assess the systematic relationships of the fossils from New Jersey, and they tentatively concluded that this taxon may be a basal member of the order Ericales. Fossils of this taxon are rare at the Allon locality.

Miscellaneous Fossil Angiosperm Flowers, Fruits, and Other Structures: Order and Family *Incertae Sedis*

29. Pentamerous flower with inferior ovary Figure 26.

The flowers are epigynous, presumably bisexual, ca. 2 mm long, 1.75 mm wide, with a pentamerous calyx (Fig. 26A). The sepal lobes are triangular with an obtuse, rounded apex. The corolla and androecium are not preserved. The hypanthium has slightly prominent longitudinal ridges. The gynoecium consists of an inferior ovary and three free styles (Fig. 26B). Pollen grains on the style surfaces are tricolporate.

These flowers are comparable in general morphology to flowers of Hydrangeaceae, Saxifragaceae, and Grossulariaceae, but currently available details are insufficient to evaluate their possible systematic relationships. Flowers of this type are very rare at the Allon locality.

30. Pentamerous flower with semi-inferior ovary Figure 27.

Flowers bisexual, 1 mm long, 0.9 mm wide, with a semi-inferior ovary (Fig. 27A, B). Calyx composed of five free sepals that are abruptly narrowed above the base (Fig. 27D); distal portions of sepals are short and blunt (Fig. 27A, D). Corolla not preserved. The androecium is composed of five stamens that alternate with five apparent staminodes (Fig. 27A, D). The five fertile stamens are opposite the sepals and have short filaments and small, dor-

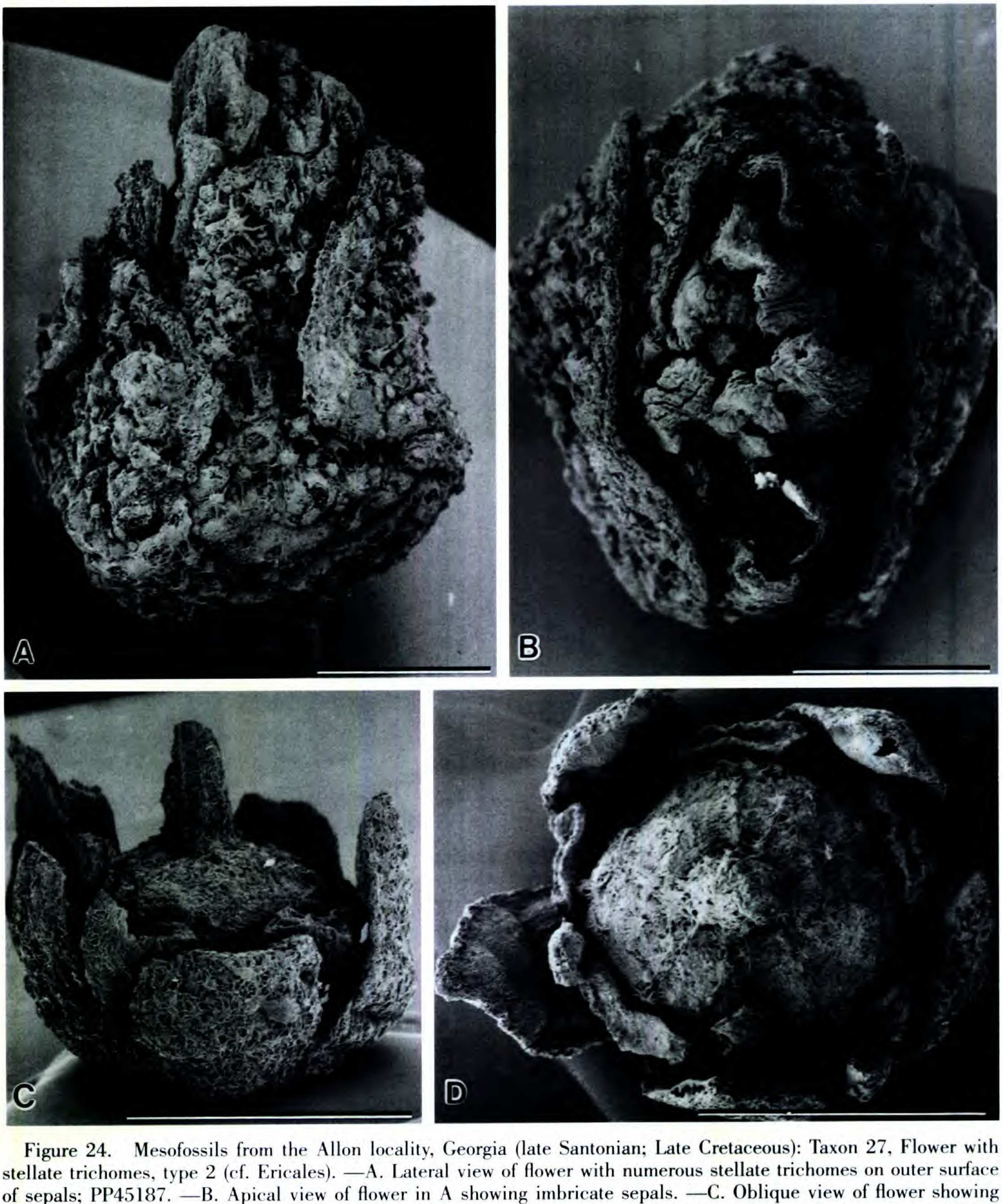

Figure 24. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 27, Flower with stellate trichomes, type 2 (cf. Ericales). —A. Lateral view of flower with numerous stellate trichomes on outer surface of sepals; PP45187. —B. Apical view of flower in A showing imbricate sepals. —C. Oblique view of flower showing remains of perianth and single style; PP45188. —D. Apical view of specimen in C showing sepals, large nectary lobes alternating with sepals, and the bases of two filaments. Scale bars = 1 mm.

sifixed anthers. The presumed staminodes (or possibly stamens that have lost their anthers) alternate with the sepals and are approximately one-third longer than the fertile stamens. The gynoecium consists of a half inferior ovary and two short styles. Locule number and mature fruit structure are unknown.

This flower is similar in some respects to *Tylerianthus crossmanensis* Gandolfo, Nixon & Crepet (1998) from the Turonian of New Jersey. However, the specimens described here differ in shape of the sepals, the dorsifixed rather than basifixed anthers, and details of in situ pollen. The abruptly narrowed sepals, stamens opposite the sepals, staminodes alternate to the sepals, and the bicarpellate half inferior ovary are all features consistent with a rela-

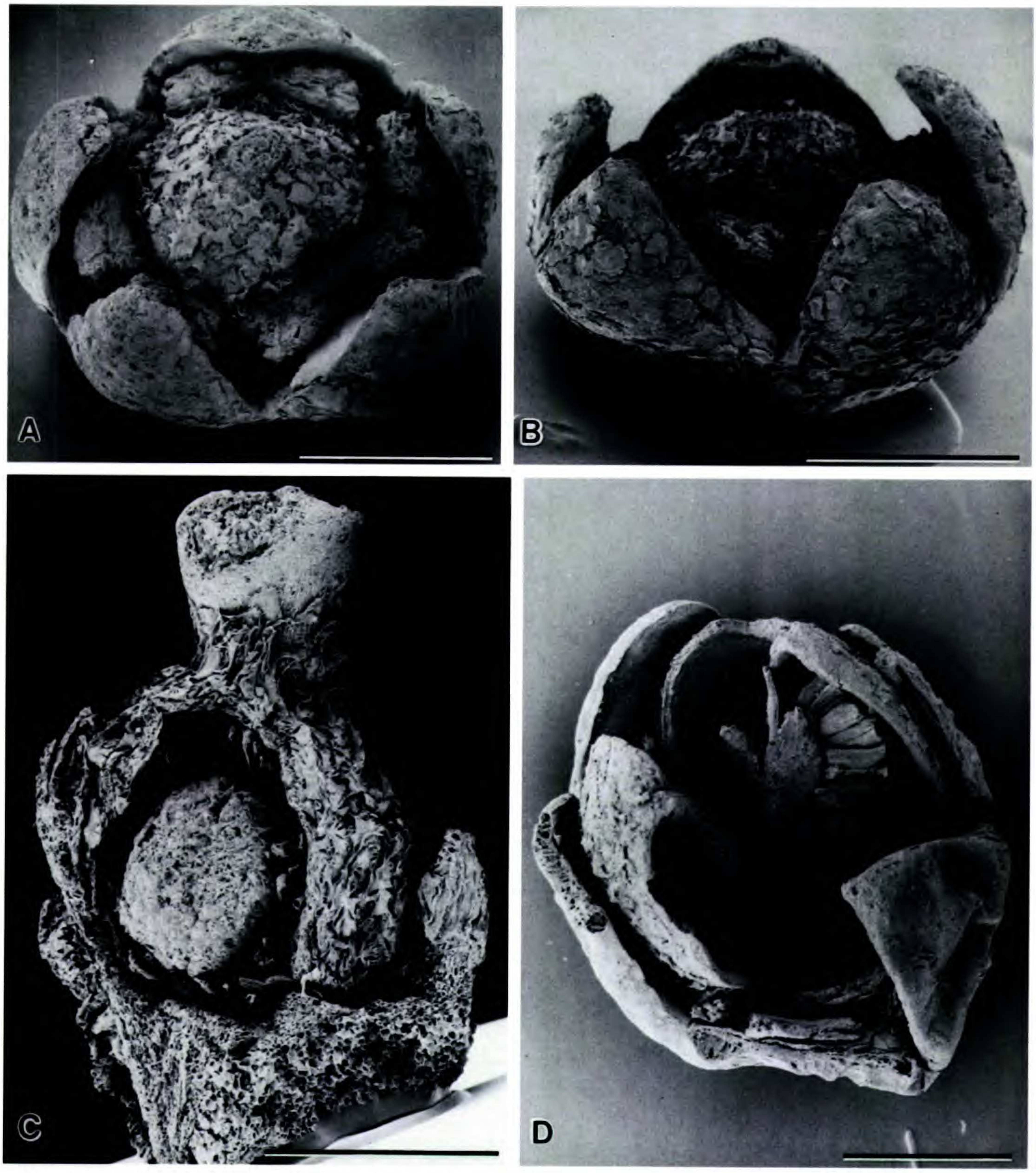

Figure 25. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 28, Fruits bearing large peltate trichomes (cf. Ericales). —A. Young fruit with five fleshy sepals and eight well-developed nectary lobes; note triangular outline of young fruit and numerous peltate trichomes on the sepals and young fruit; PP45189. —B. Lateral view of specimen in A showing peltate trichomes on sepals and ovary. —C. Abraded fruit specimen showing massive placenta and numerous ovules; note basal (united) portion of style; PP45190. —D. Mature trilocular capsule with numerous seeds and persistent sepals; note loculicidal dehiscence; PP45191. Scale bars = 1 mm.

tionship to Hydrangeaceae and Grossulariaceae. Few specimens of this taxon are known.

31. Flower with spindle-shaped inferior ovary Figure 28.

Flowers bisexual, epigynous, forming a long, spindle-shaped fruit that is 4–8 mm long. Calyx abraded, connate at least at the base, number of sepals unknown. Corolla abraded, connate at least at the base, number of petals unknown. Stamens, possibly five, enclosed within corolla (Fig. 28A, E), exserted at maturity (Fig. 28H). Filaments free, attached at base of corolla tube (Fig. 28H). Anthers apparently dorsifixed. Gynoecium composed of

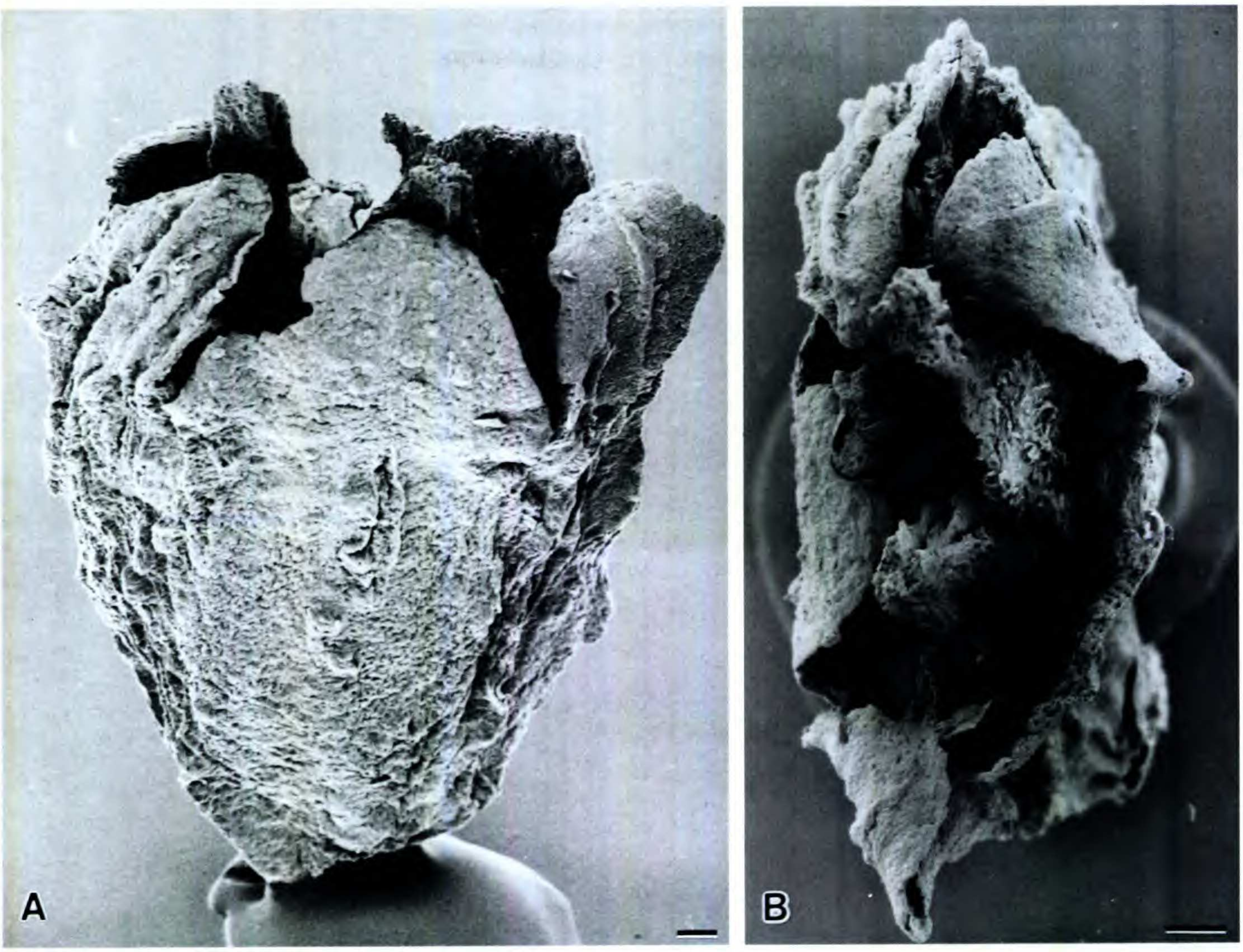

Figure 26. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 29, Pentamerous flower with inferior ovary. —A. Lateral view of flower showing inferior ovary, three styles, and five sepals; PP44603. —B. Apical view of flower in A showing three styles. Scale bars = 100 μm.

long, slender inferior ovary. Styles three, basally united, but free for most of their length and recurved at maturity (Fig. 28C, G). The stigma is decurrent on the distal third of the style. Locule and ovule number unknown. Large open pores (?modified stomata) at base of style may represent nectariferous tissue. Mature fruits are spindle-shaped with longitudinal ridges (Fig. 28B, C). Pollen grains are prolate, tricolporate, with an open reticulum that becomes closed toward the colpi.

Complete specimens of this flower have not been recovered, and details of perianth structure are poorly known. The fruits are especially abundant in the Allon samples and are almost always preserved as compressed lignitized specimens. The pollen grains are distinctive and have been found on all of the dispersed parts (Lupia et al., 1995). The flowers may have been protandrous. Some specimens are preserved with the three style lobes tightly appressed (Fig. 28D, H), while others have the style lobes recurved with the presumed stigmatic surfaces exposed (Fig. 28C, G). One specimen with appressed style lobes has an elongated filament still attached (Fig. 28H). This specimen may indicate that the stamens were exserted, and reached maturity, before the stigmatic surfaces were exposed.

These fossils are broadly similar to *Esgueiria* Friis, Pedersen & Crane (1992), which was described from the Late Cretaceous of Portugal and recently discovered also from the Late Cretaceous of Japan (Takahashi, Crane & Ando, unpublished data). Friis et al. (1992) suggested that *Esgueiria* has a close relationship with the Combretaceae (Myrtales), although free style lobes do not occur in any extant member of the family. Free style and stigma lobes are present in some other members of Myrtales. Additional details of perianth structure, and locule number, are needed for a more complete assessment of possible relationships. This morphotype is one of the five most abundant angiosperms at Allon (> 1000 whole or partial specimens) and is the only mesofossil that has also been recognized in the compression flora (Fig. 28C).

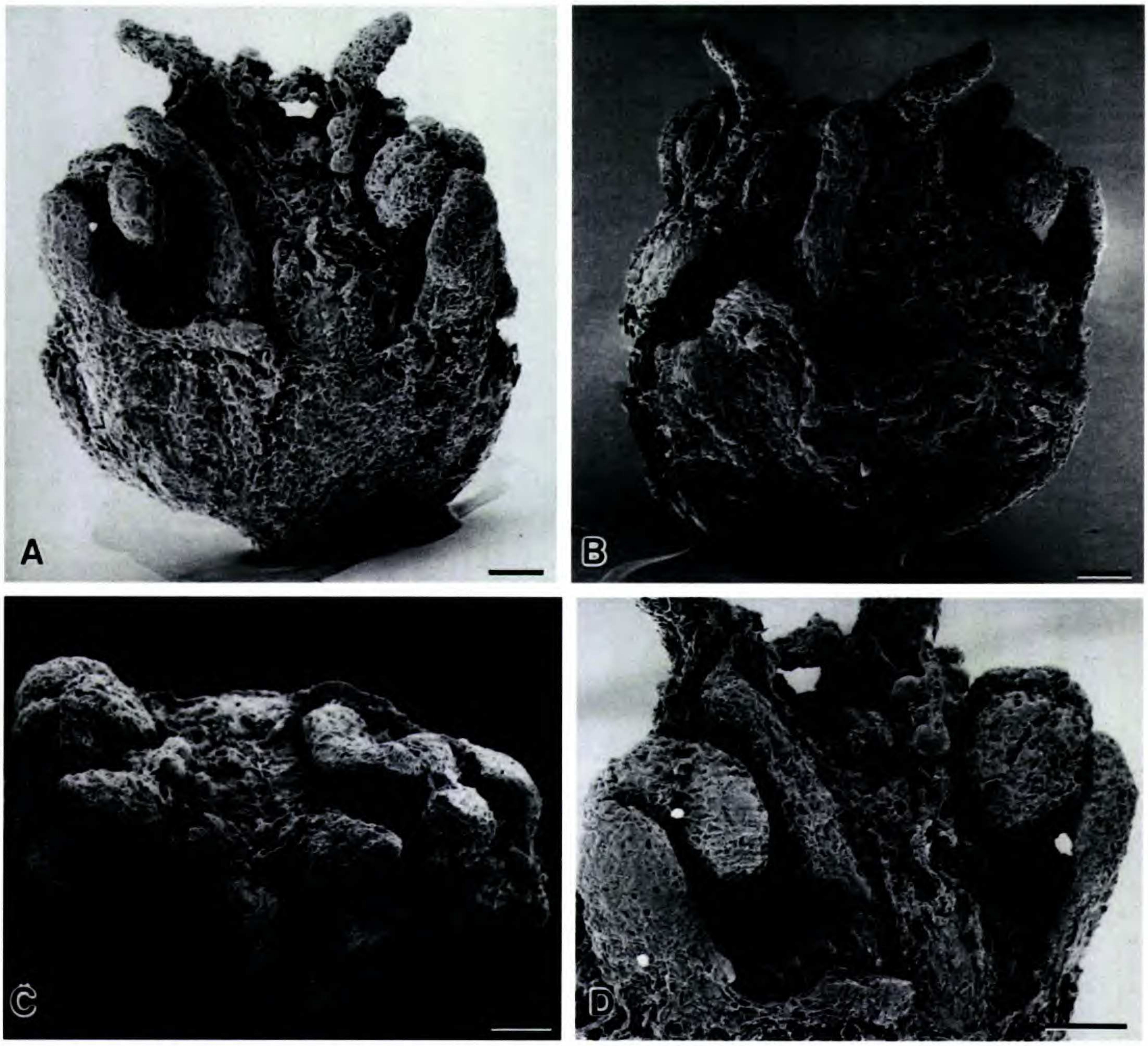

Figure 27. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 30, Pentamerous flower with semi-inferior ovary. —A. Lateral view of flower showing semi-inferior ovary, two styles, stamens with dorsifixed anthers, and long stamen filaments or staminodes; PP45192. —B. Opposite side of flower shown in A. —C. Apical view of flower shown in A. —D. Detail of flower in A showing narrow sepals and anther. Scale bars = 100 μm.

32. Flower with lobed petals
Figure 29.

Flowers bisexual, epigynous, 2 mm long, 1 mm wide. Perianth composed of a calyx, which is abraded in the available specimens, and lobed petals. Petals have either three (Fig. 29A) or two lobes (Fig. 29B). Stamen number unknown but possibly five; details of filaments and anthers unknown. Gynoecium bicarpellate with a semi-inferior ovary with two placentae and several ovules (Fig. 29E). Two short, free styles are inserted between two large, prominent, spongy structures at the apex of the ovary (Fig. 29C, D). Pollen grains are small (polar axis 6 μm), prolate, tricolporate, tectate, and microechinate. Fruits are small, triangular in outline, with a thin epidermis or epicarp that is frequently not preserved, and a thicker endocarp that dehisces to yield two valves. Mature fruits have a single locule (Fig. 29E), and apparently only a single seed develops to maturity.

One of the most distinctive features of these flowers is the large, spongy, bilobed structure that is located above the insertion of perianth and stamens (Fig. 29C, D). Two short styles are located between these structures. Most specimens are lignitized and compressed, and these structures appear as wings or a continuation of the ovary (Fig. 29A, D). However, several charcoalified specimens (e.g., Fig. 29C) clearly show that these structures are not part of the ovary. They are similar in appearance to a massive bilobed nectary disk.

The fossil flowers and fruits are similar in many respects to those of the Araliaceae and Apiaceae. A minute calyx, lobed petals, large nectary disk, bicarpellate gynoecium with an inferior ovary, and free styles are all features found in these families. However, parietal placentation and more than one ovule per locule are features not found in extant Araliaceae or Apiaceae. Additional study of the fossil specimens, and extant Araliaceae and Apiaceae, is needed before the relationships of these fossils can be understood in more detail.

This taxon is one of the five most abundant taxa in the Allon flora (> 1000 whole or partial specimens).

33. Trimerous flower with numerous coarse trichomes
Figure 30.

Flowers are slender, pedicellate, 2–3 mm long, 1–1.5 mm wide, with numerous long, coarse trichomes on all flower parts. Most specimens are abraded with perianth and androecium broken. Perianth usually composed of six tepals (Fig. 30D, E), but flowers with five tepals also occur. Tepals are narrow and taper to an acute apex (Fig. 30A, B). Stamen filaments are broken, and anthers are unknown. At least six filaments are present, but the exact number is unknown (Fig. 30C). Filaments bear numerous coarse trichomes. Some specimens contain three relatively long, slender styles; others have no evidence of styles. Other details of the gynoecium are unknown. Pollen is tricolporate, ca. 15–17 μm long, with a perforate tectum.

This flower type is very common, but it is poorly known because most specimens are broken. The long, coarse trichomes covering all surfaces are distinctive. Abraded specimens in which the trichomes have been broken have a distinctive pock-marked surface. The flowers are similar to the staminate flowers of *Antiquacupula sulcata* (taxon 21) but differ in several respects, especially the more numerous trichomes, larger pollen grains, and absence of the obvious united style base. It is possible that these flowers represent another taxon of Fagaceae sensu lato but more structural details are needed to pursue this comparison further.

34. Capitate inflorescence of pentamerous flowers
Figure 31.

Inflorescence capitate, borne terminally on a slender stalk, small, diameter ca. 1.2 mm, containing ca. 20 sessile flowers (Fig. 31A, B). Flowers small, diameter ca. 0.4 mm. Calyx composed of five free sepals with broadly rounded apices and scattered simple trichomes on the abaxial and adaxial surfaces. Internal to, and alternating with, the sepals are five long, slender structures that may be stamen filaments (Fig. 31C, D). Anthers not preserved. Pollen has not been found on the specimen. The center of the flower contains a cycle of 10 awl-shaped structures (Fig. 31B, D) that are presumed to represent the gynoecium, but details are unknown.

This inflorescence is known from a single specimen. Many aspects of the flower structure are uncertain, and additional specimens are needed for more detailed characterization.

35. Flower with pentamerous perianth and trimerous gynoecium
Figure 32.

Flowers are hypogynous, pedicellate (Fig. 32A), actinomorphic, ca. 1.2 mm in diameter. The calyx is pentamerous (Fig. 32B, D), the sepals are basally united for ca. 0.2 mm, free lobes ca. 0.7–0.8 mm long; sepal apex obtuse to acute. Corolla and androecium unknown. Gynoecium syncarpous, tricarpellate, ovary superior, locule number unknown (Fig. 32D). Single style long, slender, hollow, fluted, apex acute. Surface of ovary papillose. Pollen grains tricolporate, exine slightly rugose.

The short, broad ovary of these flowers, with a papillose surface, is one of their most distinctive features (Fig. 32C). These flowers are similar in some respects to those of some taxa in the Ericales, especially in the hollow, fluted style, but currently there is insufficient information to investigate relationships further.

36. Flower with pentamerous calyx composed of thick valvate sepals
Figure 33.

Flowers are hypogynous (Fig. 33A), actinomorphic, and possibly unisexual, 1–2 mm long, 1 mm wide. Calyx composed of five valvate, thick sepals that taper to an acute apex (Fig. 33B, C). Stamens apparently five, alternate with the sepals (Fig. 33D). Gynoecium not observed. Pollen grains are tricolporate, polar axis 12 μm, with a finely reticulate exine sculpture.

There are relatively few specimens available for this flower type, and few structural details have been documented. As a consequence, little is known regarding the possible systematic relationships of this fossil within the eudicots.

37. Slender epigynous flower
Figure 34.

Flowers slender, epigynous (Fig. 34A–C), actinomorphic, apparently bisexual, 2.4 mm long, 1 mm wide. Perianth composed of six narrow, free

Figure 28. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 31, Flower with spindle-shaped inferior ovary. —A. Lateral view of abraded flower showing stamens; PP45193. —B. Young spindle-shaped fruit showing apex of the gynoecium protruding above the remains of the perianth; PP45194. —C. Compression fossil of spindle-shaped fruit; note recurved style lobes (light micrograph); PP45151. —D. Apical portion of gynoecium

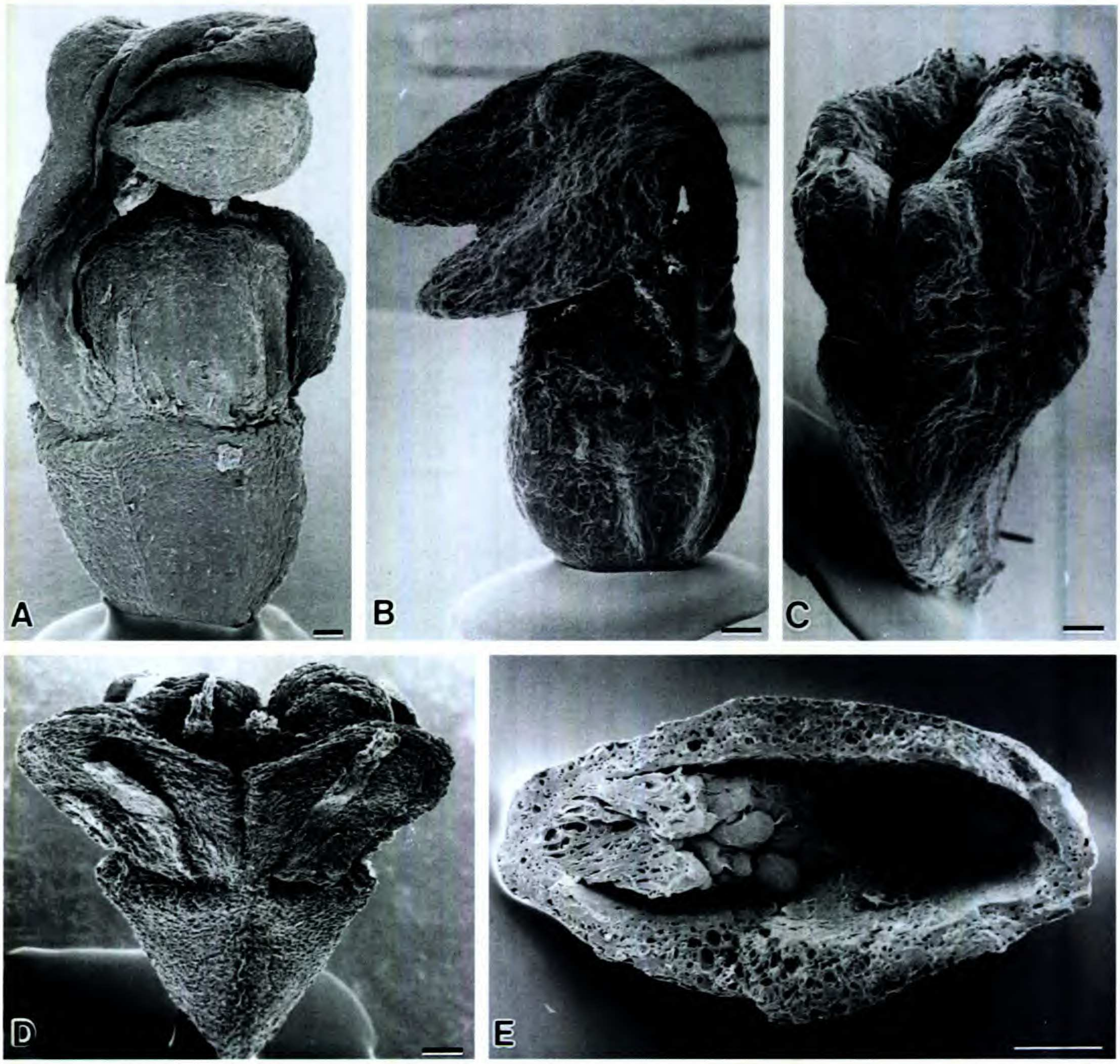

Figure 29. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 32, Flower with lobed petals. —A. Flower with one trilobed petal; PP44597. —B. Flower with one bilobed petal; PP45198. —C. Young fruit with large, bilobed nectary present; note that two short, free styles are present between nectary lobes; PP45199. —D. Flower with several stamen filaments attached; note two styles in center; PP45200. —E. Transverse fracture of fruit showing placenta along suture on left; placenta on other suture removed during preparation; PP45201. Scale bars = 100 μm.

tepals with an acute apex. Stamens 12, represented by filaments only, anthers not preserved, pollen grains unknown. Six filaments alternate with the tepals, six are opposite the tepals. Filaments are tangentially flattened and at least as long as the tepals (Fig. 34D, E). The filaments alternate with thin, slender structures (Fig. 34E). Ovary inferior, triangular in cross section with somewhat thickened corners. Styles lobes three.

These flowers are very similar to the pistillate flowers of *Antiquacupula* (taxon 21) (Sims et al., 1998) but differ in several features. The filaments

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showing remains of perianth and two of three style lobes; PP44599. —E. Oblique apical view of specimen in A showing anthers. —F. Apical view of flower showing remains of calyx tube and corolla tube; PP45195. —G. Apical portion of style showing three recurved style lobes; compare with styles in C; PP45196. —H. Oblique view of flower showing style with lobes tightly appressed and remains of stamen covered with numerous pollen grains; PP45197. Scale bars: A, D–H = 100 μm; B = 10 mm; C = 1 mm.

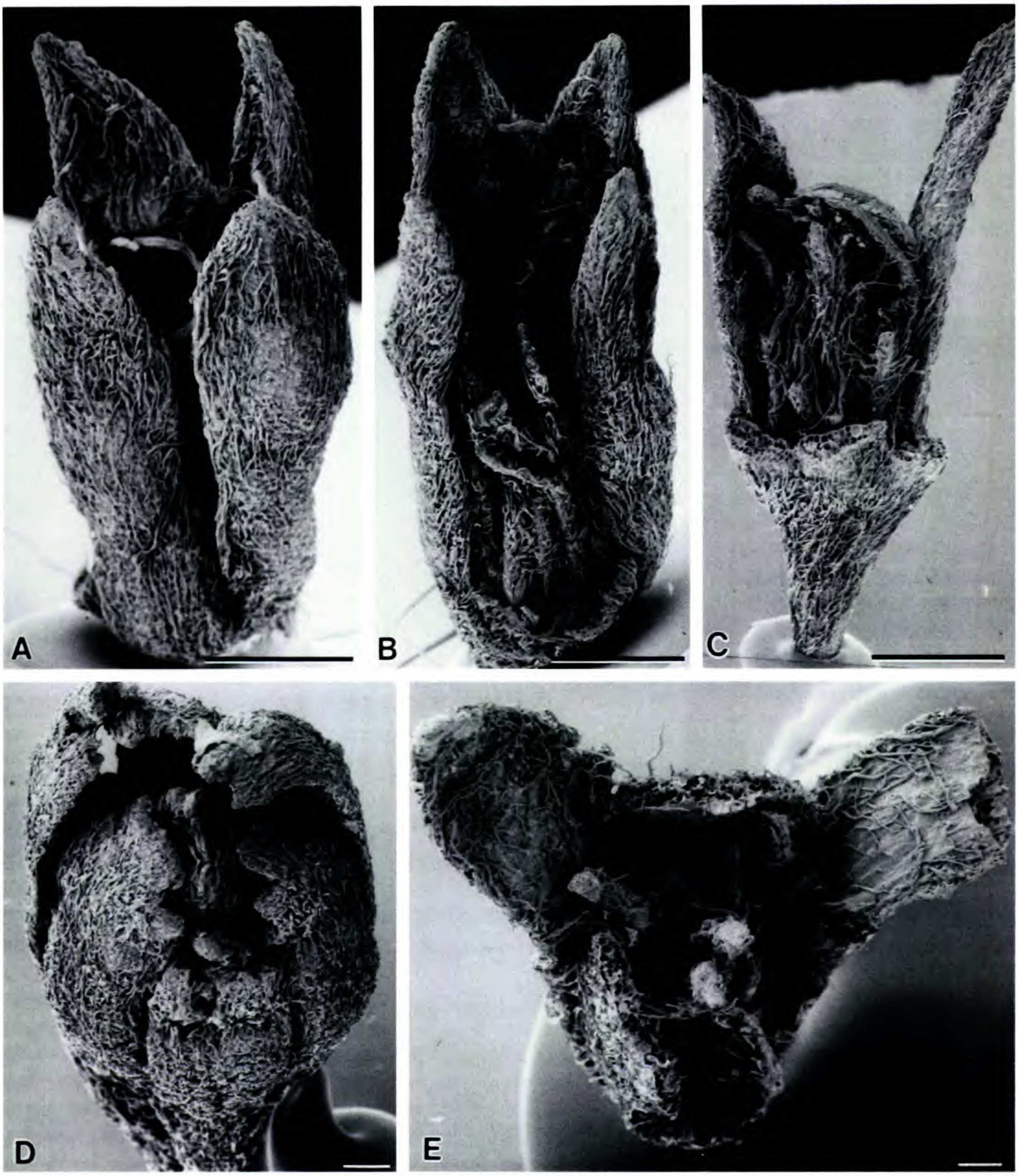


Figure 30. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 33, Trimerous flower with numerous coarse trichomes. —A. Lateral view of flower showing perianth with numerous, coarse, densely spaced trichomes; PP45202. —B. Opposite side of flower shown in A; note two perianth parts are missing, revealing several narrow filaments covered with numerous trichomes. —C. Lateral view of flower with several perianth parts removed showing several filaments and abundant trichomes; PP45203. —D. Flower bud with intact calyx comprised of six tepals; PP45204. —E. Apical view of flower showing arrangement of tepals; PP45205. Scale bars: A–C = 0.5 mm; D, E = 100 μm.

are flattened, whereas they are terete in *Antiquacupula*, and there is no evidence of swollen filament bases in these specimens, while this is a consistent feature of *Antiquacupula sulcata.* There is also no evidence of longitudinal ridges and grooves on the ovary of these specimens, whereas again, this feature is consistently observed on fruits of *Antiquacupula sulcata.* These flowers may represent a second species of *Antiquacupula,* but additional specimens and details are needed to pursue this

Figure 31. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 34, Capitate inflorescence of pentamerous flowers. —A. View of base of inflorescence showing central axis and several flowers with broken perianth; PP45206. —B. Lateral view of specimen in A, showing perianth of several flowers; flower at center has three of five sepals present. —C. Detail of specimen in A showing a single flower with five fragmentary perianth parts (?sepals), filaments, and possible gynoecium. —D. Oblique view of specimen in A showing a single flower. Scale bars = 100 μm.

possibility further. This taxon is represented in the Allon flora by only two specimens.

38. Epigynous flower with spherical ovary Figure 35.

Flowers epigynous, bisexual, apparently actinomorphic, 4.2 mm long, 2.7 mm wide (Fig. 35A, B). Perianth abraded, poorly preserved. Calyx composed of possibly five sepals. Corolla not preserved. Fusiform structures (?stamens) numerous, grouped in possibly five bundles opposite the sepals (Fig. 35B, C). Filaments of putative stamens short, anthers with an acute apical extension of the connective (Fig. 35C, D). Pollen not preserved. Gynoecium composed of a large, spherical inferior ovary and single thick style possibly with five distal free lobes (Fig. 35A, B).

This taxon is known from only one poorly preserved specimen. An inferior ovary together with numerous stamens in bundles occurs in several orders of Dilleniidae, but more structural details are needed before possible systematic relationships can be assessed.

39. Flower with very broad perianth parts and coarse fimbriate trichomes Figure 36.

Flowers hypogynous with a perianth composed of a single cycle of 4–6 tepals (commonly 5), ca. 4 mm long, 3 mm wide (Fig. 36A). Tepals very broad with prominent venation, apparently persistent in fruit. Tepals thin and foliose, glabrous, broadly rounded at the apex, with a relatively narrow base, but not clawed. Androecium and pollen grains not

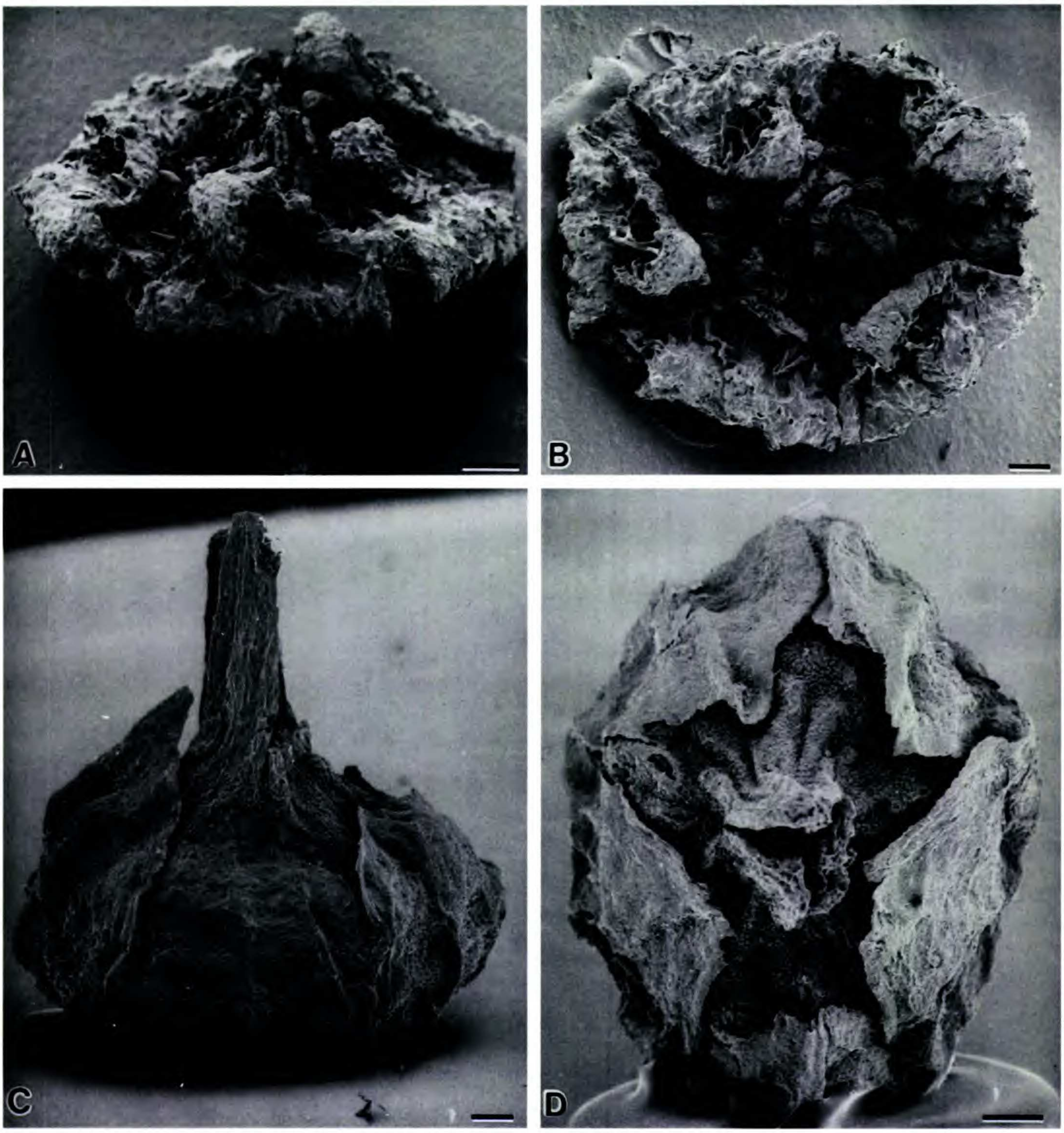


Figure 32. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 35, Flower with pentamerous perianth and trimerous gynoecium. —A. Lateral view of vertically compressed flower showing pedicel and thin sepals; PP45207. —B. Apical view of specimen in A showing pentamerous calyx. —C. Lateral view of flower showing imbricate sepals and long style; PP45208. —D. Apical view of flower showing hollow style and papillose surface of the ovary; PP45209. Scale bars = 100 μm.

preserved. Gynoecium composed of a superior ovary with three locules and three free, but confluent, styles (Fig. 36B). The surface of the ovary is covered by numerous large, coarse, fimbriate trichomes (Fig. 36C). The fruits are loculicidal capsules, with at least two seeds per locule (Fig. 36D).

This taxon is represented by several hundred specimens, nearly all of which are preserved as compressed lignitized material rather than as charcoal. None of the specimens provide any evidence of an androecium, and no staminate flowers are known from the Allon flora that have a comparable perianth. Although specimens of this taxon are abundant, they currently provide insufficient structural details to evaluate systematic relationships.

40. Ovate fruit
Figure 37.

Fruits derived from a superior ovary, ovate, 3–4 mm long, 3.0–3.5 mm wide, with an acute apex bearing a single style scar (Fig. 37A, B). Fruits apparently unilocular with partial septae. Ovule

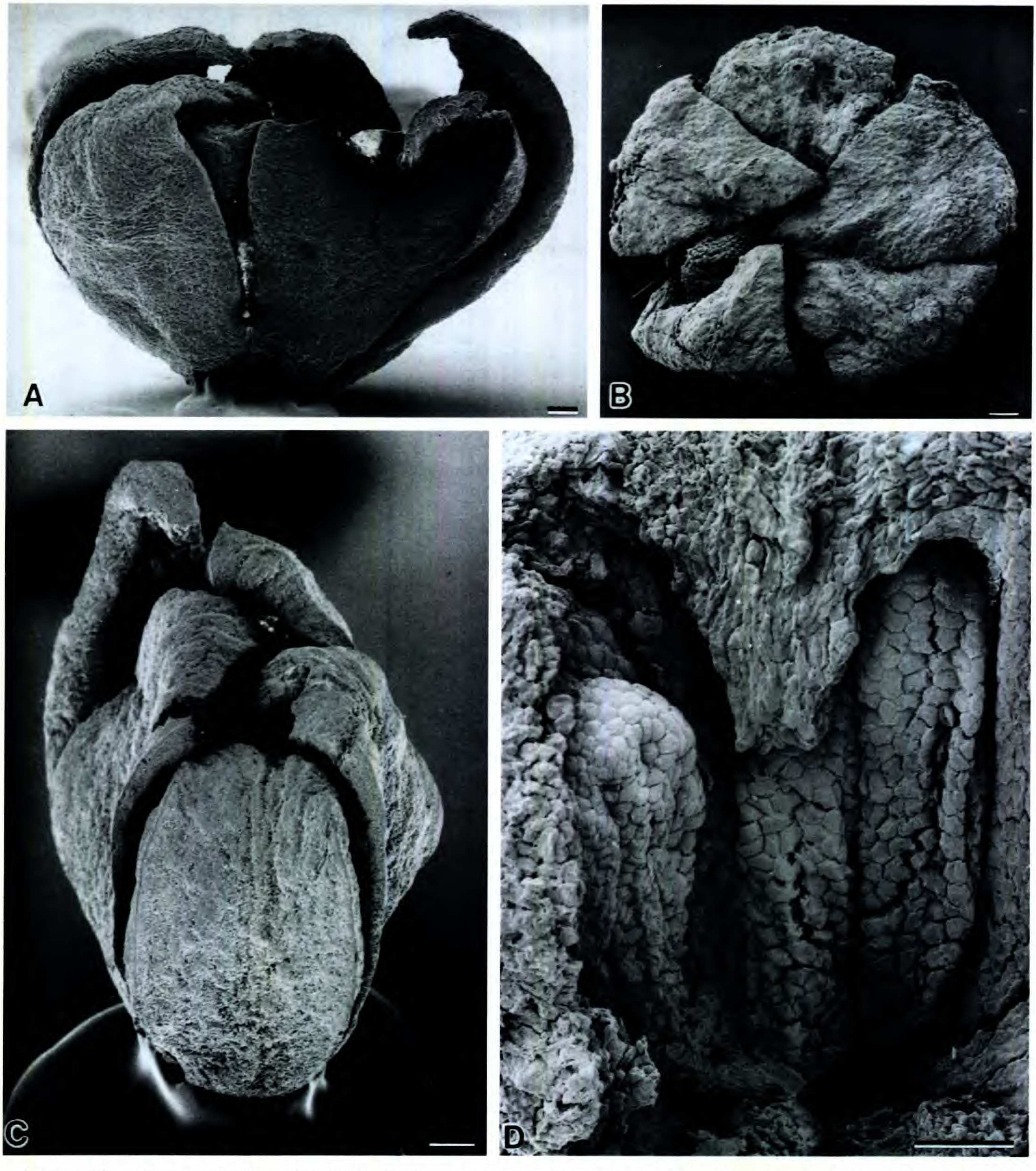
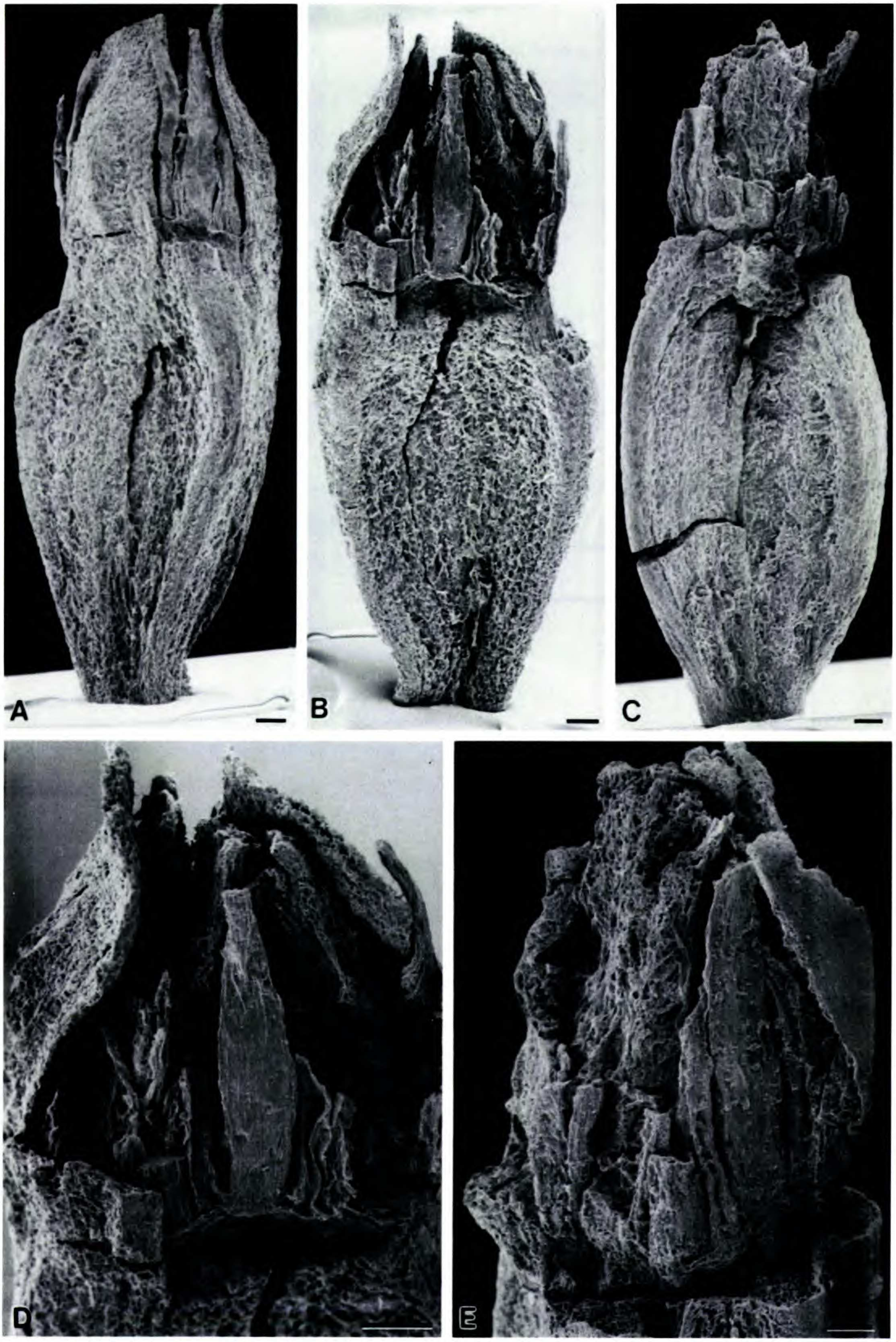


Figure 33. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 36, Flower with pentamerous calyx composed of thick, valvate sepals. —A. Lateral view of flower showing valvate sepals with acute apices; PP45210. —B. Apical view of flower showing sepals with acute apices; PP45211. —C. Oblique view of flower showing thick, valvate sepals; PP45212. —D. Flower with broken perianth revealing anthers; PP45213. Scale bars = 100 μm.

and seed number are unknown. The fruit wall apparently consisted of a fleshy outer layer and a more resistant endocarp. The endocarp is characterized by the presence of lacunae that are clearly visible externally but apparently do not connect with the locule (Fig. 37D). The fruit wall is marked by three prominent longitudinal ribs that extend from base to apex. Nine less well developed ribs are also present, three between each major rib, and these generally do not extend all the way to the fruit apex. A poorly preserved perianth is present in some specimens (Fig. 37A). The perianth is apparently trimerous, but the quality of preservation is insufficient to confirm this feature.

This morphotype is one of the five most abundant angiosperms at Allon (> 1000 whole or partial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specimens). However, there are insufficient distinctive characters to determine systematic relationships for this fossil fruit. The fruits are usually preserved as laterally compressed specimens (Fig. 37A, B), but a few charcoalified, three-dimensional specimens are also present in the Allon assemblage (Fig. 37D).

41. Bicarpellate superior fruit
Figure 38.

Fruits ca. 2.25 mm long, 1.75 mm wide, 1 mm thick, apparently derived from a superior ovary, lenticular, bicarpellate with two persistent style bases. Locule, ovule, seed, and pollen details are unknown. Possible perianth remnants are preserved on the base of one specimen (Fig. 38A).

This fruit type is known from two poorly preserved specimens, one of which is very abraded (Fig. 38B). The fruit is apparently derived from a superior ovary because remains of a perianth are present on one specimen (Fig. 38A). This feature confirms that this fruit is not the same as the lenticular fruit of *Protofagacea.* This fruit type is similar in many features to specimens from Upatoi Creek in western Georgia (Herendeen et al., unpublished data). Absence of pollen precludes comparisons with fossils bearing Normapolles pollen and relevant extant taxa. Additional material is needed before this taxon can be understood in more detail.

42. Epigynous flower with rounded sepals
Figure 39.

Flowers are epigynous, apparently actinomorphic, 3.5–3.7 mm long, 2.5 mm wide, with a pentamerous calyx composed of short, broadly rounded sepal lobes, and a gynoecium with a single style. The ovary and calyx are covered by numerous short, blunt trichomes. Corolla and androecium are not preserved. Details of ovary structure are unknown.

This flower type is represented by only a few poorly preserved specimens. The short, blunt, and often downwardly directed, trichomes are distinctive and have not been observed in other fossils from the Allon locality. Additional better preserved specimens are needed before systematic relationships can be evaluated.

43. Pentamerous flower with bracteoles
Figure 40.

Flowers are pedicellate, subtended by a pair of fleshy bracteoles (Fig. 40A, B), hypogynous, apparently actinomorphic, ca. 1.5 mm long, and 1.5 mm wide. The calyx is pentamerous, basally united for ca. 1/3 of its length, thick and fleshy except at the margins of the free lobes (Fig. 40C). Ovary composed of five carpels, superior, locule number unknown. There is a single style scar present at the apex of the ovary in a slight depression (Fig. 40C, D). Corolla and androecium are not preserved.

Only a single specimen of this taxon is known. The style appears to have been inserted in a slight depression in the apex of the ovary. This feature is commonly present in flowers of Ericales. The calyx structure, gynoecium of five carpels, and the presence of paired bracteoles are also consistent with a relationship to Ericales. Additional details, especially of corolla and androecium, are needed for a more precise assessment of the systematic relationships of this fossil.

44. Immature bicarpellate fruit
Figure 41.

Flower epigynous with a thick hypanthium cup, which has small conical protuberances on its inner wall and slight longitudinal ribbing externally toward the base. Gynoecium bicarpellate, composed of a single inferior ovary and two free but confluent styles. The styles are shorter than the hypanthium cup. Details of perianth and androecium are unknown.

This fossil is known from a single incomplete specimen of an immature fruit. The thick, well-developed hypanthium cup is distinctive. No other details are known for this fossil.

45. Inflorescence with trimerous flowers
Figure 42.

Inflorescence pedunculate, cymose, bearing flower buds with a trimerous perianth. Flower buds are 0.8 mm long and 0.4 mm wide. The peduncle is short and thick (Fig. 42B, C). At the apex of the

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Figure 34. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 37, Slender epigynous flower. —A. Lateral view of flower showing inferior ovary and perianth; PP45214. —B. Opposite side of specimen in A with perianth removed showing filaments flanked by narrow, thin-walled structures. —C. Specimen with abraded perianth; PP45215. —D. Detail of specimen in A and B showing perianth, flattened filaments, and thin-walled structures alternating with the filaments. —E. Detail of specimen in C showing perianth, flattened filaments, and thin structures alternating with the filaments. Scale bars = 100 μm.

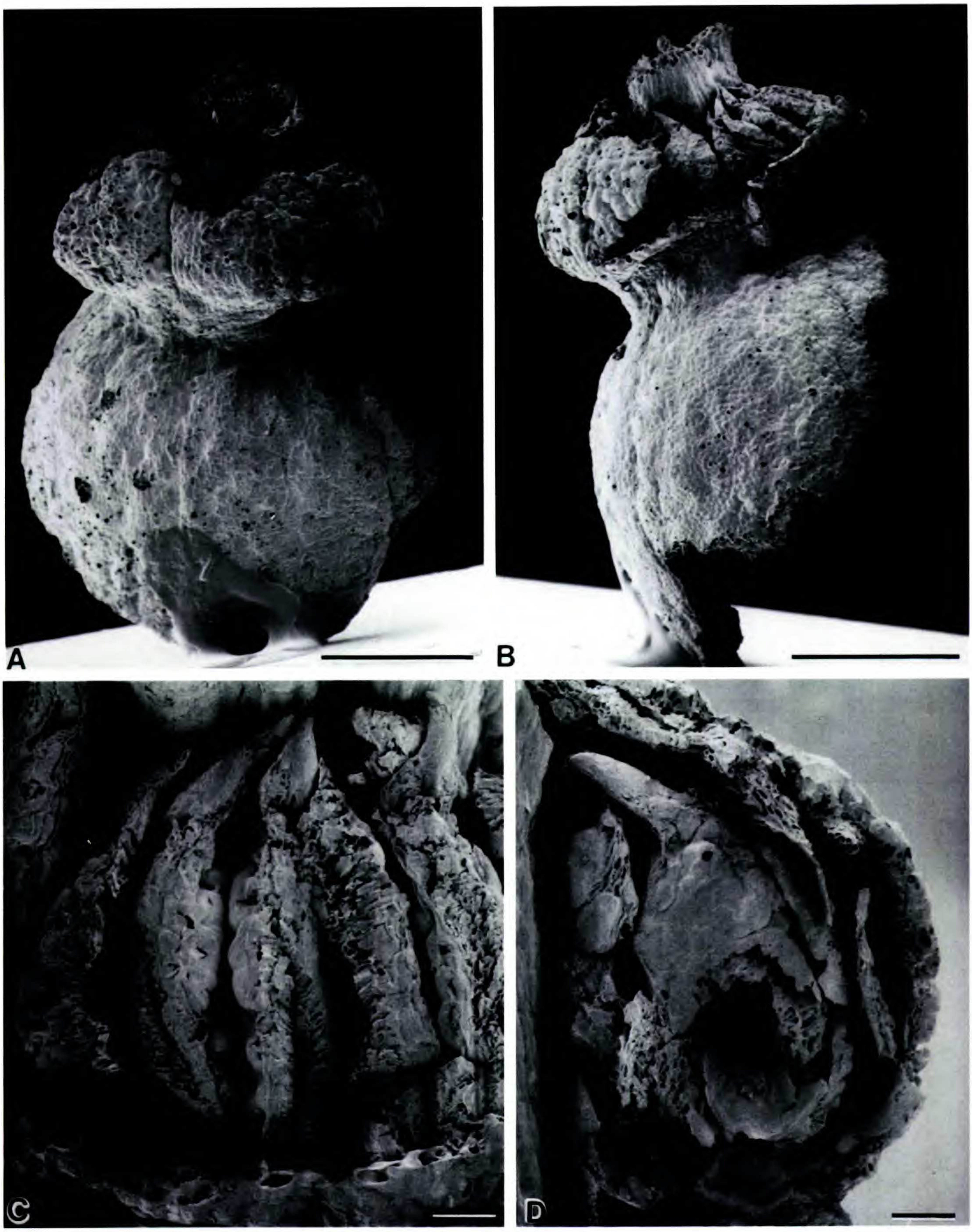


Figure 35. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 38, Epigynous flower with spherical ovary. —A. Lateral view of flower showing ovary and sepals; PP45216. —B. Specimen in A showing broken ovary, clusters of stamens opposite two sepals, and base of thick style. —C. Detail of abraded stamens showing connective extension. —D. Lateral view of stamen showing connective extension. Scale bars: A, B = 1 mm; C, D = 100 μm.

Figure 36. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 39, Flower with very broad perianth parts and coarse trichomes. —A. Lateral view of flower showing perianth; PP45217. —B. Oblique view showing broad perianth members and three free styles; PP45218. —C. Flower with perianth parts removed to show superior ovary covered with coarse trichomes; PP45219. —D. Longitudinally fractured fruit showing ovules in situ; PP45220. Scale bars = 1 mm.

peduncle there is a single flower pedicel, flanked by two clusters of flowers that are subtended by digitately divided bracts (Fig. 42D). Most flowers are broken off, and their position is indicated by pedicel bases only. The organization of the lateral groups of flowers is difficult to discern because the flowers are tightly clustered. In some specimens the lateral clusters appear to have a cymose organization. Flower buds, pedicels, and bracts are all covered by numerous simple trichomes.

The flower buds that are present on some specimens are too small to dissect for internal structural details, and no specimens with larger flowers attached are available. The flower buds are somewhat similar in gross morphology and trichome structure to young staminate flowers of *Antiquacupula sulcata* (taxon 21; Sims et al., 1998, fig. 4), but it has not yet been possible to compare details of flower structure. Because there are other pedicellate flowers with trimerous perianth and long simple trichomes

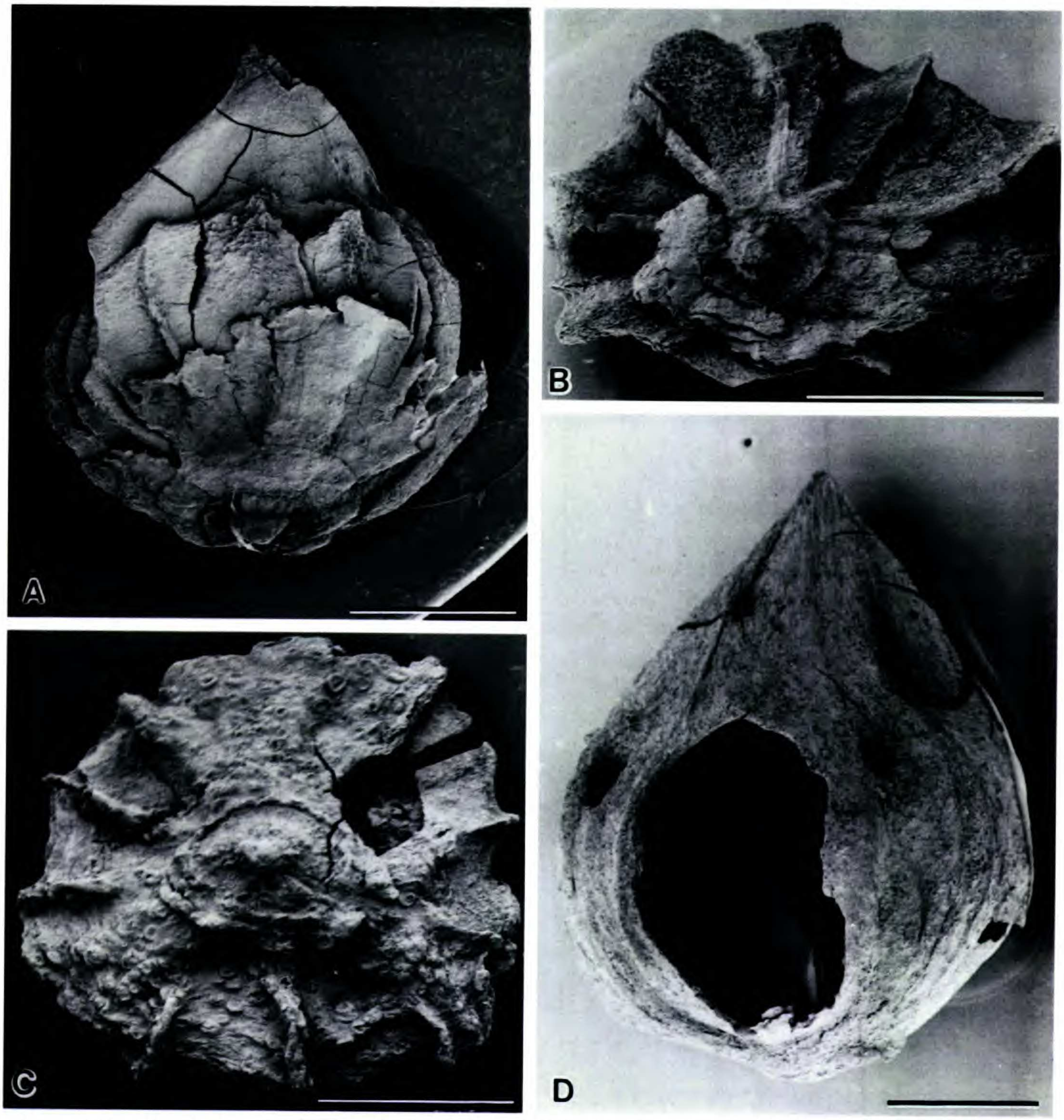


Figure 37. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 40, Ovate fruit. —A. Lateral view of endocarp with remains of other fruit layers and perianth; PP45221. —B. Base of fruit showing attachment scar, remains of perianth, and fleshy tissue adhering to endocarp; PP45222. —C. Basal view of fruit showing attachment scar and remains of perianth; note numerous small spherical structures (?galls) on surface; PP45223. —D. Lateral view of endocarp with broken fruit wall showing locule; note lacunae in endocarp; PP45224. Scale bars = 1 mm.

in the Allon flora, it is premature to associate this fossil with *Antiquacupula sulcata*. The cymose organization with bracts subtending the lateral flowers is consistent with inflorescence structure in Fagaceae sensu lato. This taxon is common in the Allon assemblage.

46. Strobiloid spicate axis
Figure 43A, B.

Axis fragment 2 mm long, 1.7 mm wide, fleshy in appearance, with helically arranged scars (Fig. 43A). The axis bears approximately 40 round attachment scars, each of which is flanked by two flange-like structures (Fig. 43B). No other structural details are available.

This taxon is known from only a single specimen. It is not certain that this taxon is an angiosperm.

47. Spherical capitate inflorescence
Figure 43C, D.

Capitate inflorescence on pedunculate axis. The specimen is 9 mm long. The presumed inflores-

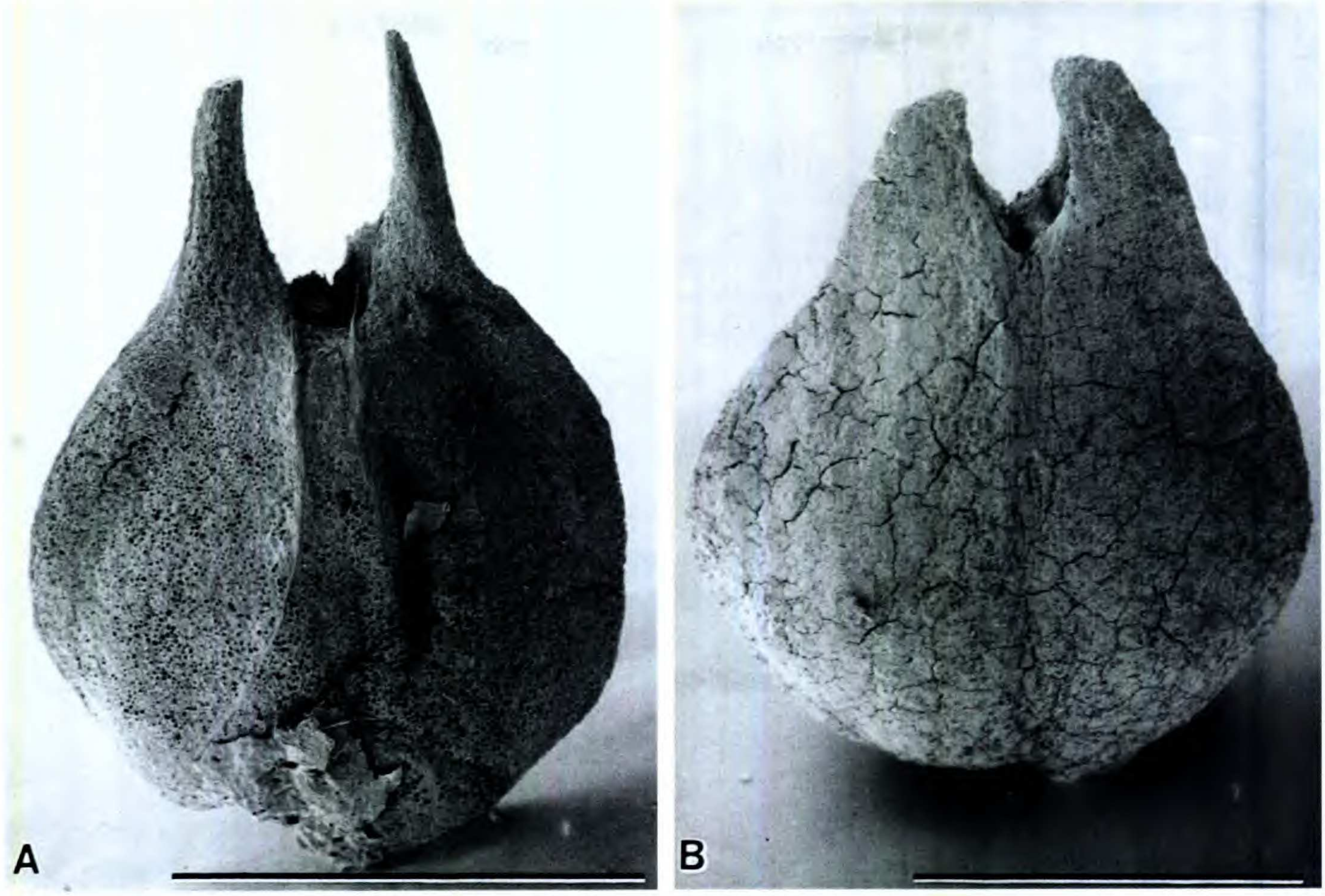


Figure 38. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 41, Bicarpellate superior fruit. —A. Lateral view of specimen showing two style bases and remains of perianth; PP45225. —B. Lateral view of abraded fruit; PP45226. Scale bars = 1 mm.

cence is represented by a spherical cluster of numerous presumed pedicel bases interspersed with trichomes (Fig. 43D).

The single specimen is severely abraded, and other structural details are unknown.

48. Miscellaneous axes with attached leaves/bracts, type 1
Figure 44A–C.

There are two types of axes bearing closely spaced, helically arranged leaves/bracts. The first (taxon 48, Fig. 44A–C) has numerous, gradually tapering leaves (or bracts), each of which subtends a three-parted axillary structure (Fig. 44C). The leaves/bracts are entire-margined with scattered simple trichomes on the abaxial surface and margins. The shoot axis is longitudinally furrowed with raised peg-like leaf bases (Fig. 44B, C). The axillary structures included under type 1 may include more than one taxon but are too immature or poorly preserved to determine key structural details.

49. Miscellaneous axes with attached leaves/bracts, type 2
Figure 44D, E.

The second axis type (taxon 49, Fig. 44D, E) has numerous, abruptly apically narrowed leaves (or bracts), each of which subtends one to several rounded structures, the details of which are unclear from the available material. The leaves are entire-margined with scattered simple trichomes on the abaxial surface and margins.

Axis type 2 shares some similarities with axis type 1 (taxon 48), but they differ most noticeably in the form of the leaves/bracts. It is uncertain whether this structure was produced by an angiosperm.

50. Axis with pinnate bracts
Figure 45.

The axis is 1.7 mm long, 0.7 mm wide, and bears bracts (or leaves) of two forms. The basalmost structure on the axis is a pinnately divided bract with numerous narrow, finger-like "pinnae" (Fig. 45A). The other leaves on the axis are simple and entire-margined (Fig. 45B). The central (distal) portion of the axis bears numerous smaller, narrower entire-margined structures. The margins and abaxial surfaces of all bracts/leaves support numerous simple trichomes. Internal anatomy of the axis is unknown.

This axis is known from only a single specimen. The pinnately divided structure is similar in some respects to the preserved young leaves of fern leaf type 1 (taxon 4, Fig. 4).

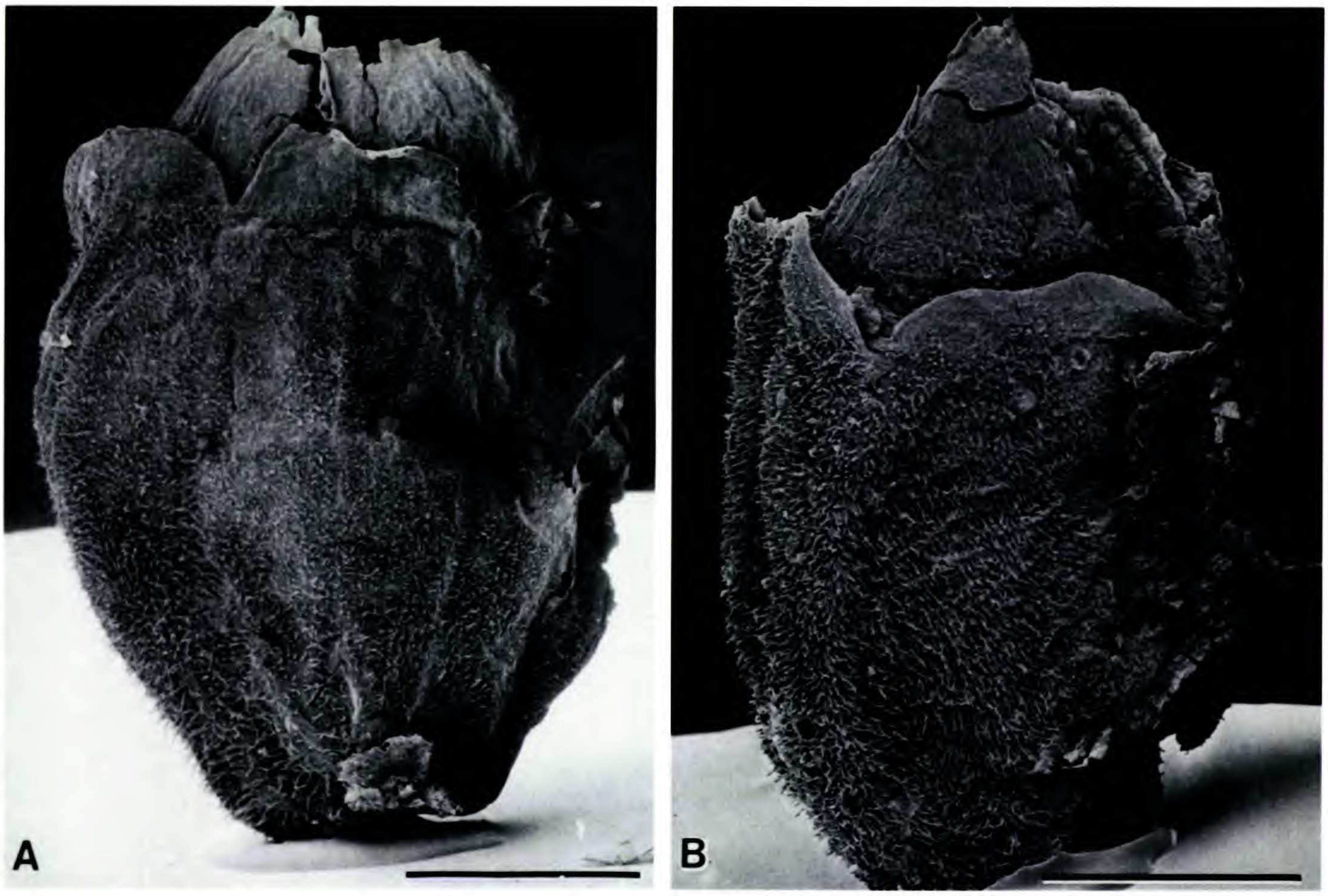


Figure 39. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 42, Epigynous flower with rounded sepals. —A. Lateral view of flower showing inferior ovary and rounded sepal lobes; note numerous short trichomes covering surface of ovary; PP45227. —B. Lateral view of flower; PP45228. Scale bars = 1 mm.

Several types of dispersed seeds are known from the Allon flora. We describe and illustrate three types that are among the most common in the Allon assemblage.

51. Miscellaneous seed type 1
Figure 46A.

Small seed with characteristic exfoliating outer cell layer of seed coat (taxon 51, Fig. 46A). Seeds are ovate, ca. 1 mm long, and 0.5–0.6 mm wide. The seed coat must have been fleshy or corky because most specimens are preserved with an outer layer that is exfoliating to reveal the cellular pattern underneath. This seed has not been found in any of the fruits that have been recovered with seeds in situ.

52. Miscellaneous seed type 2
Figure 46B.

Large seed with oblique fissure lines (taxon 52, Fig. 46B). The seeds are oblong, relatively large, ca. 2.5 mm long, 1.3 mm wide, with characteristic oblique fissure lines (Fig. 46B, arrows) that demarcate two presumed abortive seeds. One end of the seed is symmetrical, rounded, and obtuse, the other end is nearly acute and asymmetrical with a flattened face on one side (Fig. 46B). The two oblique fissures demarcate one large central section and two small flanking sections (Fig. 46B). The three sections often separate near the obtuse end of the seed. The overall structure has the appearance of a single seed with a gross morphology comparable to seeds of Hamamelidaceae subfamily Hamamelidoideae. This seed is common in the Allon assemblage but has not yet been found in a fruit.

53. Miscellaneous seed type 3
Figure 46C.

Large seed with finely pitted surface (taxon 53, Fig. 46C). This seed is oval with one end more broadly rounded than the other, relatively large, 2.5 mm long, 1.5 mm wide. The seed coat has a distinctive pitted surface. No specimens have been recovered in situ.

A great variety of non-reproductive plant parts are commonly encountered in mesofossil assemblages such as Allon, including pieces of wood and bark, leaves, bracts, and sometimes roots. We illustrate here a selection of bracts and fossil roots from the Allon assemblage.

54. Bracts
Figure 47A–D.

Bracts are represented in a diversity of morphologies. The more distinctive ones have margins that are deeply incised or toothed (taxon 54, Fig. 47A–D). One distinctive form is a relatively large, bilaterally symmetrical structure that is deeply incised with ca. 11 slender digitate processes that are 1.0–1.5 mm long with a swollen tip (Fig. 47A). The swollen structures appear to be glandular. These specimens are similar to bracts found in some species of Hamamelidoideae (Endress, pers. comm., 1998). Another specimen (Fig. 47B) is similar but has fewer digitate lobes and appears to be pinnate rather than palmate. The tips of the lobes are broken so it is unknown whether there were glandular structures present. Other bracts are asymmetrical with a margin that bears slender acute teeth (Fig. 47C). There is also a rounded form with numerous triangular teeth (Fig. 47D). Unless bracts have a very distinctive morphology, or are found attached to an axis that bears reproductive structures, it will be difficult to identify these structures.

55. Root with nodules?
Figure 47E, F.

Among the other dispersed plant parts recovered at Allon, several specimens that appear to be nodulated roots are especially interesting (taxon 55, Fig. 47E, F). The root is slender, ca. 0.15 mm in diameter, and bears clusters of oblong nodules. In one specimen (Fig. 47E) there is a cluster of four nodules that are 1 mm long, 0.3 mm wide, with a blunt, rounded apex. Another specimen bears at least six nodules that have a constriction near the apex (Fig. 47F). Unfortunately, details are insufficient to determine the systematic relationships of these roots.

56. Dicot leaf type 1
Figure 48A.

Leaf narrowly elliptical, up to 230 mm long, 45 mm wide. Base acute. Petiole unknown. Apex attenuate. Margin entire. Midrib curved, gradually thinning and becoming very fine toward the leaf apex. Secondary veins pinnately arranged, not prominent, apparently eucamptodromous. Tertiary and quaternary venation not visible.

This species resembles several leaf forms from the Middendorf and Eutaw Formations that were assigned by Berry (1914) to the extant genera *Ficus* or *Laurus*, but the accuracy of these determinations remains uncertain. This leaf is one of two leaf types (see also taxon 57) that is abundant in the Allon macrofossil assemblage.

57. Dicot leaf type 2
Figure 48B.

Leaf narrowly elliptical, maximum length (estimated) ca. 150–200 mm (distal portion unknown), maximum width ca. 25–31 mm. Base decurrent into a broad petiole (length unknown). Margin entire. Venation pinnate. Midrib very broad at the base, tapering distally. Secondary veins diverging at angles of ca. 40°, widely spaced at intervals of up to 10 mm sometimes with intersecondaries not prominent. Tertiary venation fine, not strongly developed. Quaternary venation not visible.

This leaf type is one of the two most abundant leaf forms in the Allon macrofossil assemblage. Details of venation and its systematic relationships are unknown.

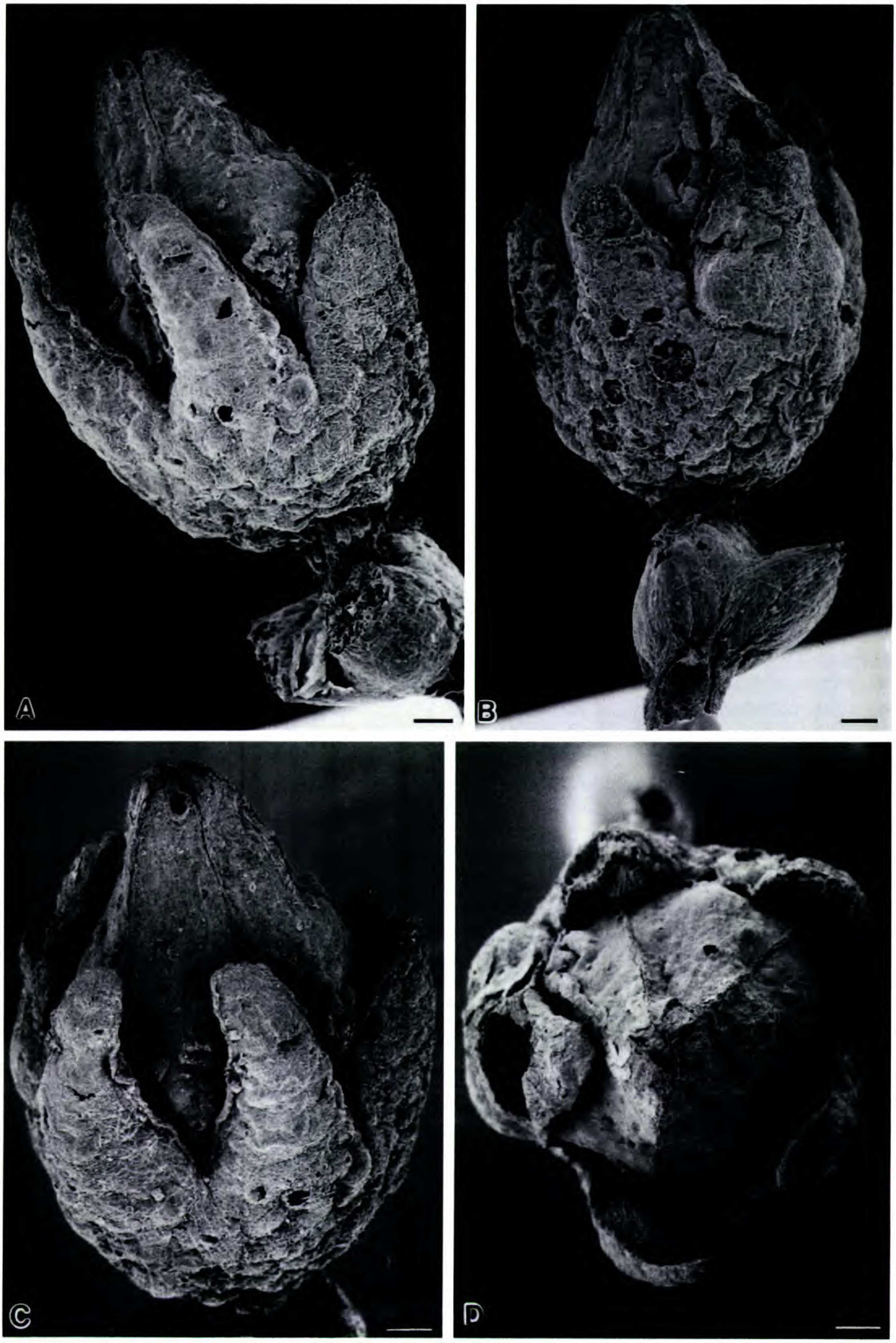
58. Dicot leaf type 3
Figure 48C.

Leaf narrowly elliptical, up to 50 mm long, 13 mm wide. Base acute. Apex acute. Margin entire. Venation acrodromous with three primary veins diverging at the leaf base and becoming thinner distally. Two additional weak secondary veins also diverge at the leaf base and run just inside the leaf margin in the distal third of the leaf. Lateral primary veins persist for more than two-thirds of the distance to the leaf apex. Secondary veins not prominent, best developed in the distal third of the leaf, especially between the outer primary veins and the leaf margin where they diverge at angles of ca. 60°. Tertiary and quaternary venation not visible.

This leaf type is similar to *Cinnamomum middendorfensis* Berry (1914, pl. 9, fig. 1) from the Middendorf and Eutaw Formations of Georgia. The yellowish coloration of these specimens may indicate that they possessed a thicker cuticle than most of the other leaves in life. This is often a feature of lauraceous leaves in other fossil leaf floras, and despite the occurrence of lauraceous reproductive structures at Allon (taxon 12), Berry's systematic determination should nevertheless be treated with caution. This leaf type is common in the Allon macrofossil assemblage.

59. Dicot leaf type 4
Figure 48D.

Leaf broadly elliptical, maximum length ca. 60 mm (incomplete), maximum width ca. 40 mm (details of base and apex unknown). Margin entire. Leaf texture thin. Venation pinnate, eucamptodromous with widely spaced secondary veins diverging at an angle of about 60° from the midrib. Prominent tertiary veins (intersecondaries) diverge from the midrib between the secondary veins and form a poorly organized, more or less orthogonal, reticulum of tertiary and quaternary veins. Ultimate venation not visible.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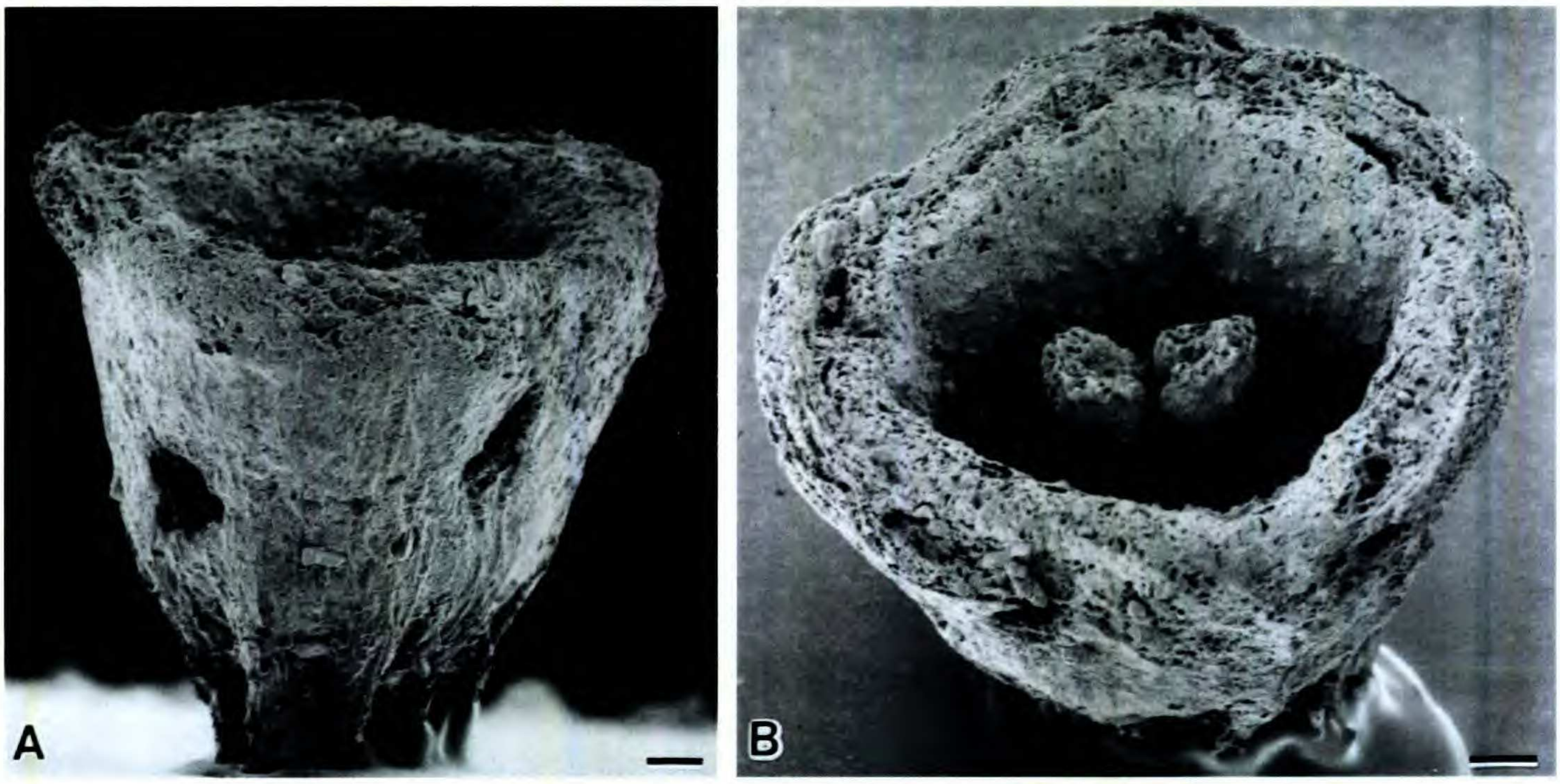

Figure 41. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 44, Immature bicarpellate fruit. —A. Lateral view of young fruit showing slight longitudinal ribbing in the basal region of the hypanthium; PP45231. —B. Oblique view of specimen in A showing two short styles inside the very thick hypanthium cup. Scale bars = 100 μm.

This leaf type is represented in the Allon macrofossil assemblage by a single specimen. The pattern of venation, in so far as it can be compared, is similar to that in leaf type 7 (taxon 62, fig. 49B). The systematic affinities of leaf type 4 are uncertain.

60. Dicot leaf type 5
Figure 48E.

Leaf of medium size, at least 100 mm in maximum length (incomplete), ca. 60 mm in maximum width (details of base, apex, and margin not preserved). Midrib prominent with a pair of strong secondaries on either side that diverge close to the leaf base. Lowermost secondary veins not prominent and diverging at angles of ca. 60° well above the leaf base. Tertiary and quaternary venation not observed.

This leaf type is rare in the Allon macrofossil assemblage. Its systematic affinities are uncertain.

61. Dicot leaf type 6
Figure 49A.

Leaf broadly elliptical or ovate. Estimated leaf length ca. 50 mm (incomplete). Maximum width ca. 25 mm. Base rounded. Petiole short (ca. 4 mm long) (leaf apex not preserved). Margin finely serrate with small, bluntly rounded teeth separated by bluntly rounded sinuses. Venation pinnate. Secondary veins thin, straight, slightly curved toward the leaf apex; diverging from the midrib at ca. 40°; regularly spaced at intervals of about 5 mm. Tertiary venation forming a poorly organized, more or less orthogonal network weakly percurrent between the secondaries. Details of tertiary and quaternary venation not observed.

The teeth on the specimen are difficult to interpret. On one side they appear distinct with a dark glandular tip, whereas on the other side the margin is irregular and perhaps damaged by insect feeding. The systematic affinities of this leaf type are uncertain. It is represented by a single specimen in the collection.

62. Dicot leaf type 7
Figure 49B.

Leaf elliptical to ovate, up to ca. 60 mm long (incomplete), up to ca. 23 mm wide. Base unknown. Apex acute to attenuate. Leaf margin entire. Ve-

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Figure 40. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 43, Pentamerous flower with bracteoles. —A. Lateral view of flower showing sepals, superior ovary, and paired bracteoles subtending flower; PP45230. —B. Opposite side of flower in A. —C. Oblique view of flower in A showing partially united calyx with acute sepal lobes. —D. Apical view of flower in A showing superior ovary with longitudinal ridges demarcating five carpels. Scale bars = 100 μm.

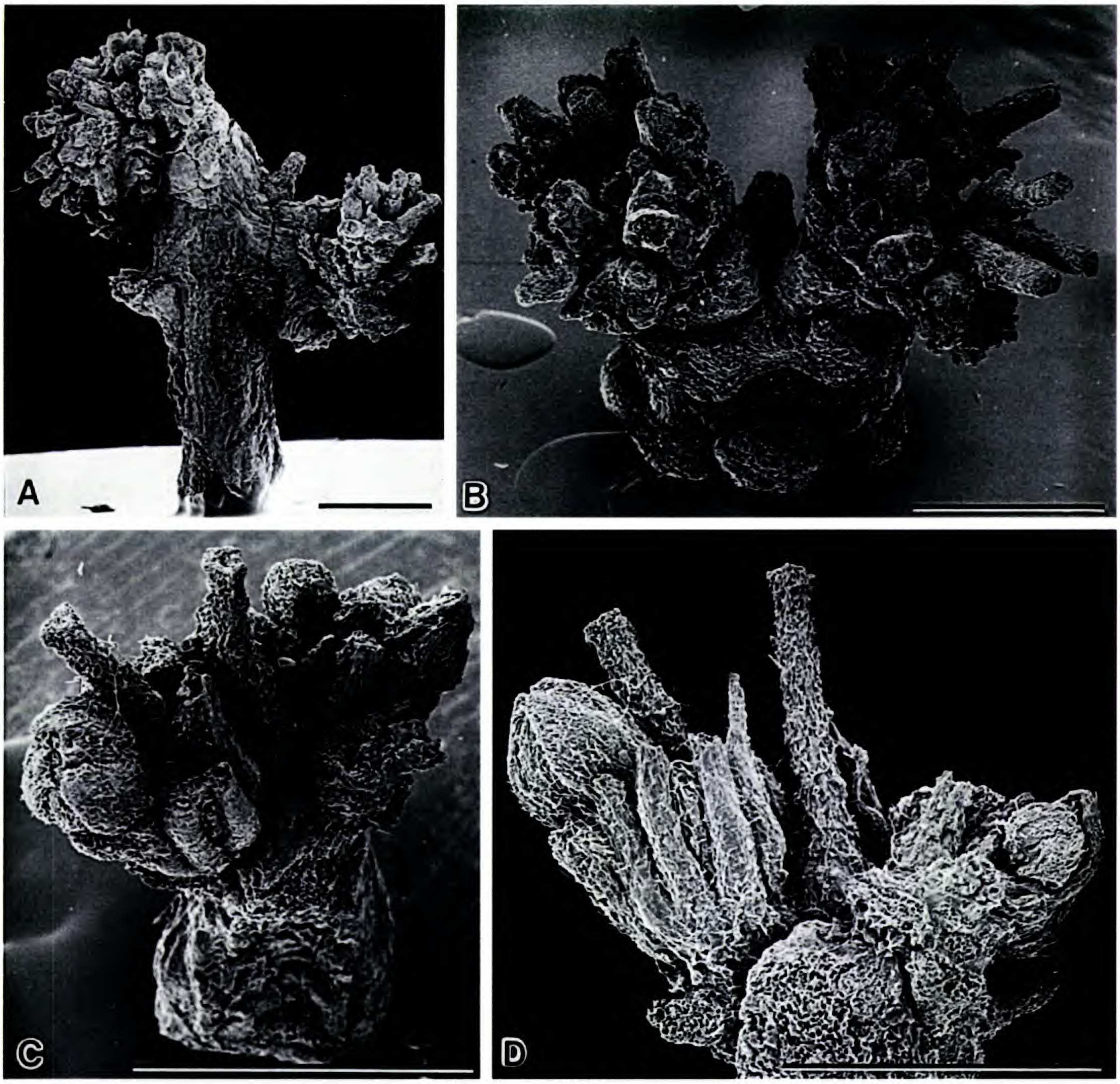

Figure 42. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 45, Inflorescence with trimerous flowers. —A. Lateral view of inflorescence with two clusters of pedicel bases; PP45233. —B. Oblique view of specimen showing cymose organization consisting of a central pedicel base and two lateral inflorescence units; note flowers are broken and only pedicel bases remain; PP45234. —C. Oblique view of inflorescence with lateral flower bud present; PP45235. —D. Lateral view of specimen in C showing flower bud subtended by a digitately divided bract. Scale bars = 1 mm.

nation pinnate, eucamptodromous. Secondary veins gently curved toward the leaf apexes, widely spaced, and diverging from the midrib at intervals of ca. 10 mm. Tertiary veins (intersecondaries) also diverge from the midrib between the major secondaries. Tertiary venation forming an irregular, more or less orthogonal network. Details of quaternary venation not observed.

This leaf type is very rare in the Allon macroflora. In general form this leaf is similar to *Diospyros* aff. *primaeva* described by Berry (1914, pl. 14, figs. 12–13) from the Santonian Middendorf and Eutaw Formations of Georgia, although this systematic determination should be treated with caution. This leaf type is similar to, and potentially conspecific with, taxon 59, leaf type 4 (Fig. 48D).

63. Dicot leaf type 8
Figure 49C.

Leaf elliptical to narrowly elliptical, estimated up to ca. 90 mm long (incomplete), width ca. 24 mm (apex and base unknown). Margin entire. Venation pinnate, eucamptodromous to weakly brochidodromous. Midrib prominent. Secondary veins fine, diverging from the midrib at angles of ca. 30–40°, straight to irregular in their course, branching

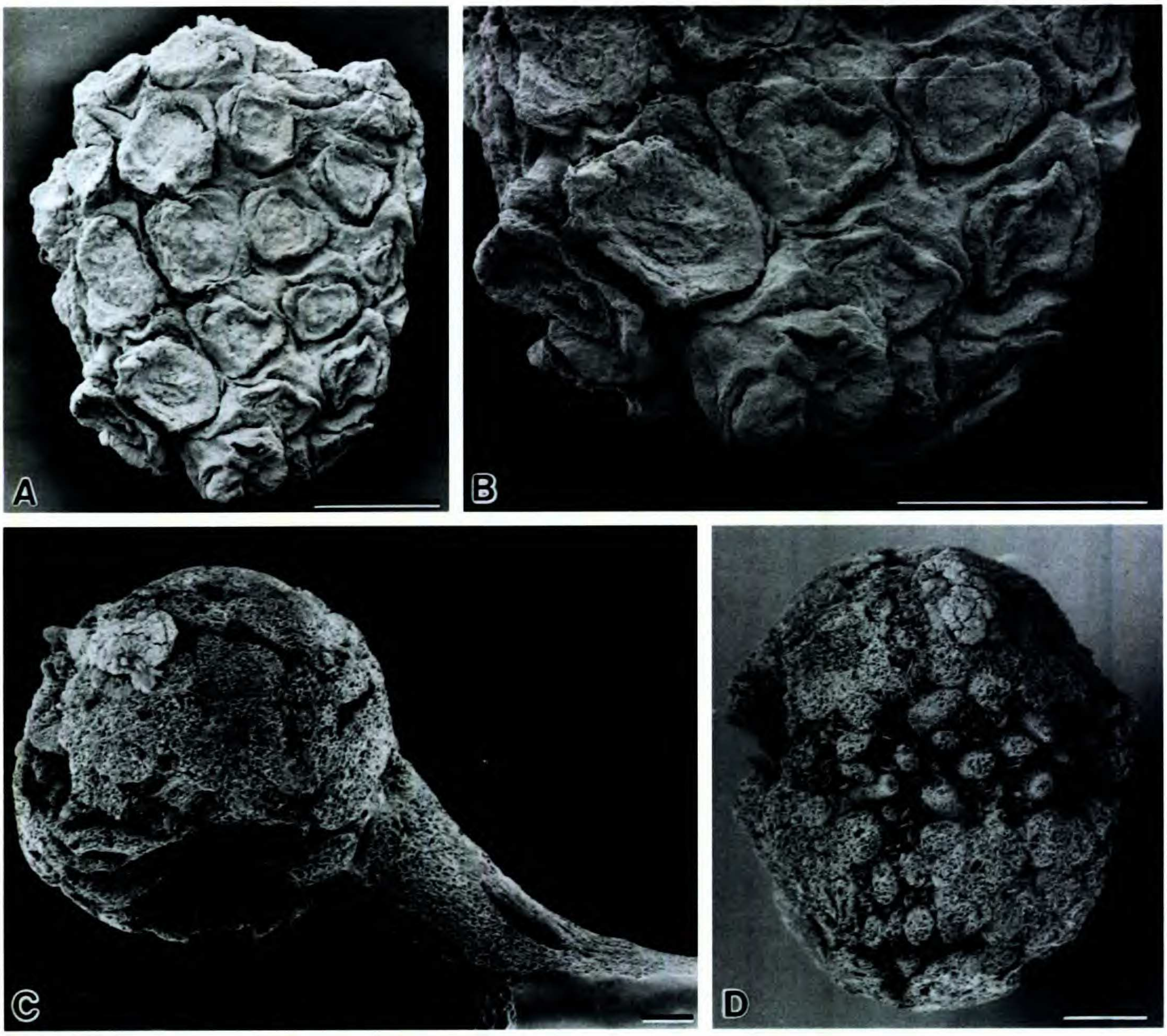

Figure 43. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxa 46 and 47, Miscellaneous reproductive axes. —A. Taxon 46, Strobiloid spicate axis; PP45236. —B. Taxon 46, Detail of specimen in A; note each scar has two flanking flange-like structures. —C. Taxon 47, Spherical capitate reproductive axis; PP45237. —D. Taxon 47, Apical view of head from specimen in C showing numerous presumed pedicel bases. Scale bars = 0.5 mm.

toward the margin to form a more or less irregular, orthogonal, network of tertiary veins, which is also developed between the secondaries. Quaternary and ultimate venation not observed.

This leaf type is very rare in the Allon macroflora, and its systematic affinities are uncertain.

Discussion

The late Santonian Allon flora from central Georgia, U.S.A., is one of many mesofossil assemblages known from the Barremian-Aptian to the Maastrichtian of North America, Europe, central Asia, and Japan (Crane & Herendeen, 1996; Friis & Skarby, 1982; Friis, 1983; Friis et al., 1999; Crepet, 1996; Takahashi, Crane & Ando, unpublished data), but it is the first to be described almost in its entirety. Systematically, the excellent preservation of flowers, fruits, seeds, and other organs provides detailed information for comparison with extant plants. Ecologically, a survey of the entire mesofossil assemblage (Table 1) provides insights into the composition of the living vegetation from which the Allon flora was derived, and a basis for estimating the abundance of the constituent taxa. Some of the taxa are known in detail, and systematic relationships are well resolved (e.g., *Parasaurauia*, Keller et al., 1996; *Allonia*, Magallón-Puebla et al., 1996; *Campylopodium*, Konopka et al., 1998), while others remain poorly characterized and their systematic relationships are unknown. Many of these fossils may never be understood in sufficient detail to justify a separate detailed treat-

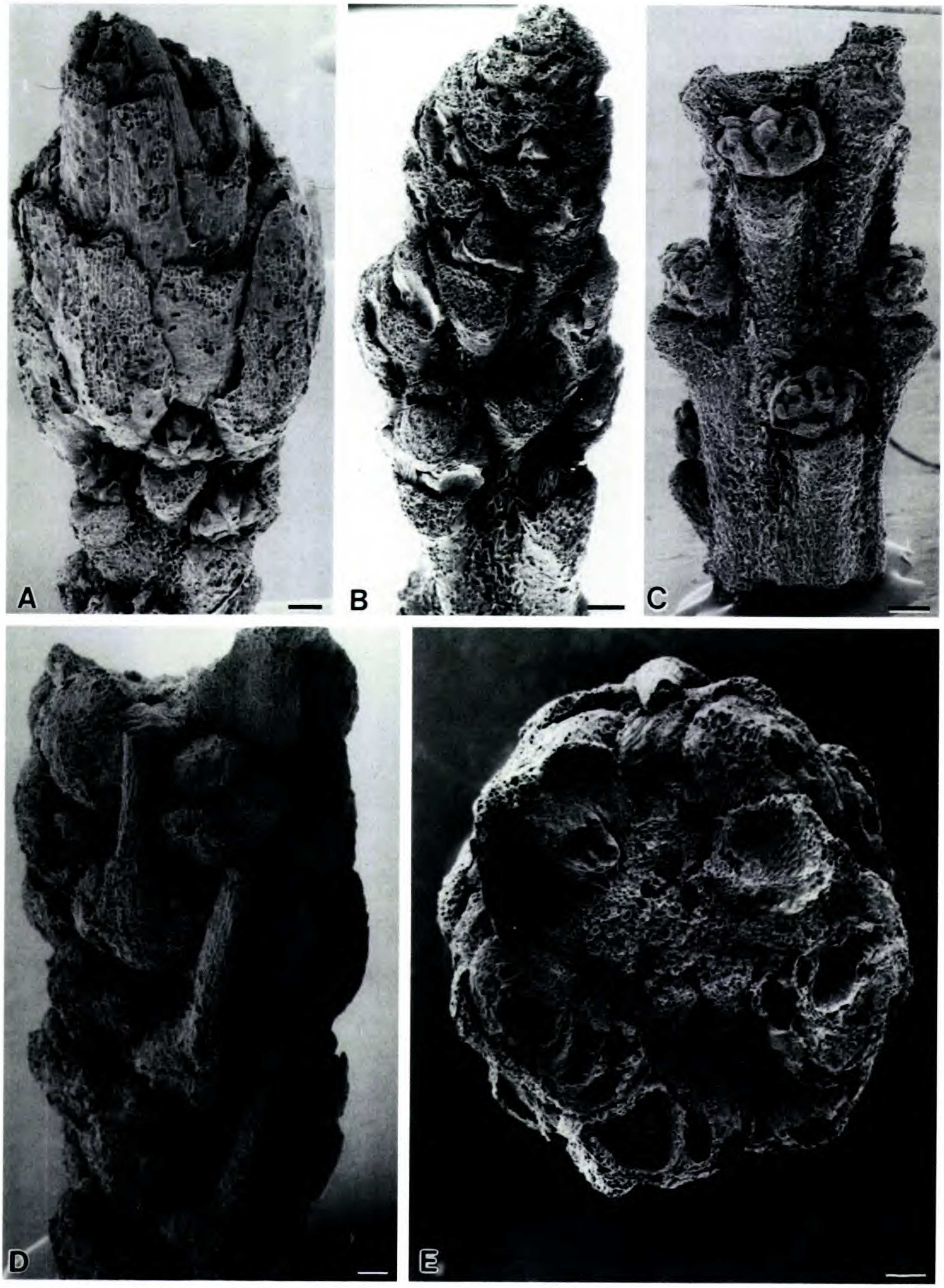

Figure 44. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxa 48 and 49, Miscellaneous axes with attached leaves/bracts. —A. Taxon 48, Axis Type 1, Oblique view of axis with bracts/leaves at apex and scars below; PP45238. —B. Taxon 48, Axis Type 1, Lateral view of axis showing broken bases of bracts/leaves; PP45239. —C. Taxon 48, Axis Type 1, Axis showing leaves/bracts with bulbous structures in their axils; PP45240. —D. Taxon 49, Axis Type 2, Axis bearing bracts/leaves that have an abruptly narrowed apex; PP45241. —E. Taxon 49, Axis Type 2, Apical view of specimen in D. Scale bars = 100 μm.

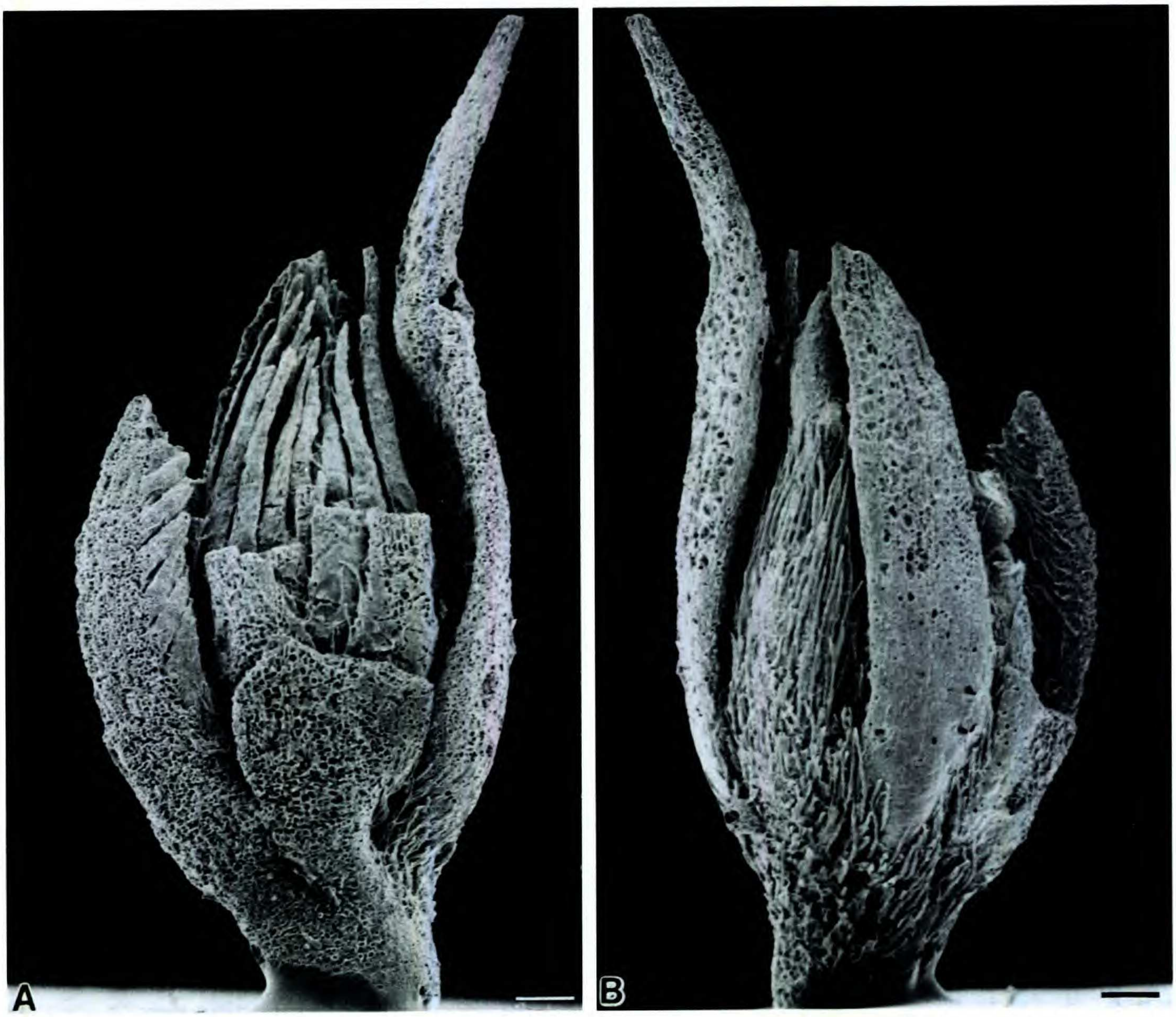

Figure 45. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxon 50, Axis with pinnate bracts. —A. Lateral view of axis with pinnate bract (left) and entire bract (right); note numerous awl-shaped structures at center; PP45242. —B. Opposite side of axis shown in A. Scale bars = 100 μm.

ment, but they may nevertheless be important for systematic, paleoecological, and biogeographic comparisons with other mesofossil assemblages.

Studies of mesofossil assemblages have greatly expanded our knowledge of Late Cretaceous plants from southeastern North America and until recently, studies of Late Cretaceous fossil plants from this area have focused almost entirely on leaves (Berry, 1914, 1919, 1925) or palynomorphs (e.g., Christopher, 1978; Frederiksen & Christopher, 1978). Mesofossils were first described from the Black Creek Formation, exposed in the "Neuse River Cut-Off" near Goldsboro, North Carolina (Friis, 1988; Friis et al., 1988; Frumin & Friis, 1996), from plant-bearing sediments considered to be of early Campanian age (Owens & Sohl, 1989). Although perhaps slightly older (late Santonian), the Allon assemblage from central Georgia is similar in many respects to that from Neuse River. The Allon assemblage is also approximately contemporaneous with the fossil leaf floras described by Berry (1914) from the Middendorf Arkose Member of the Black Creek Formation in South Carolina (now Middendorf Formation; Gohn, 1992), and the two floras may share several leaf species (Berry, 1914). Some of the Allon macrofossils are also similar to species from the Eutaw Formation (Berry, 1914, 1919), which is of early Santonian age (Huddlestun & Hetrick, 1991), probably slightly older than the Allon assemblage. Well-preserved mesofossil floras from early Coniacian sediments along Upatoi Creek in western Georgia are currently under study (Magallón-Puebla et al., 1997; Herendeen & Crane, unpublished). The Allon assemblage also shares several taxa with the older Turonian-age Crossman flora from New Jersey.

In relation to other fossil assemblages from southeastern North America, the Allon flora is older

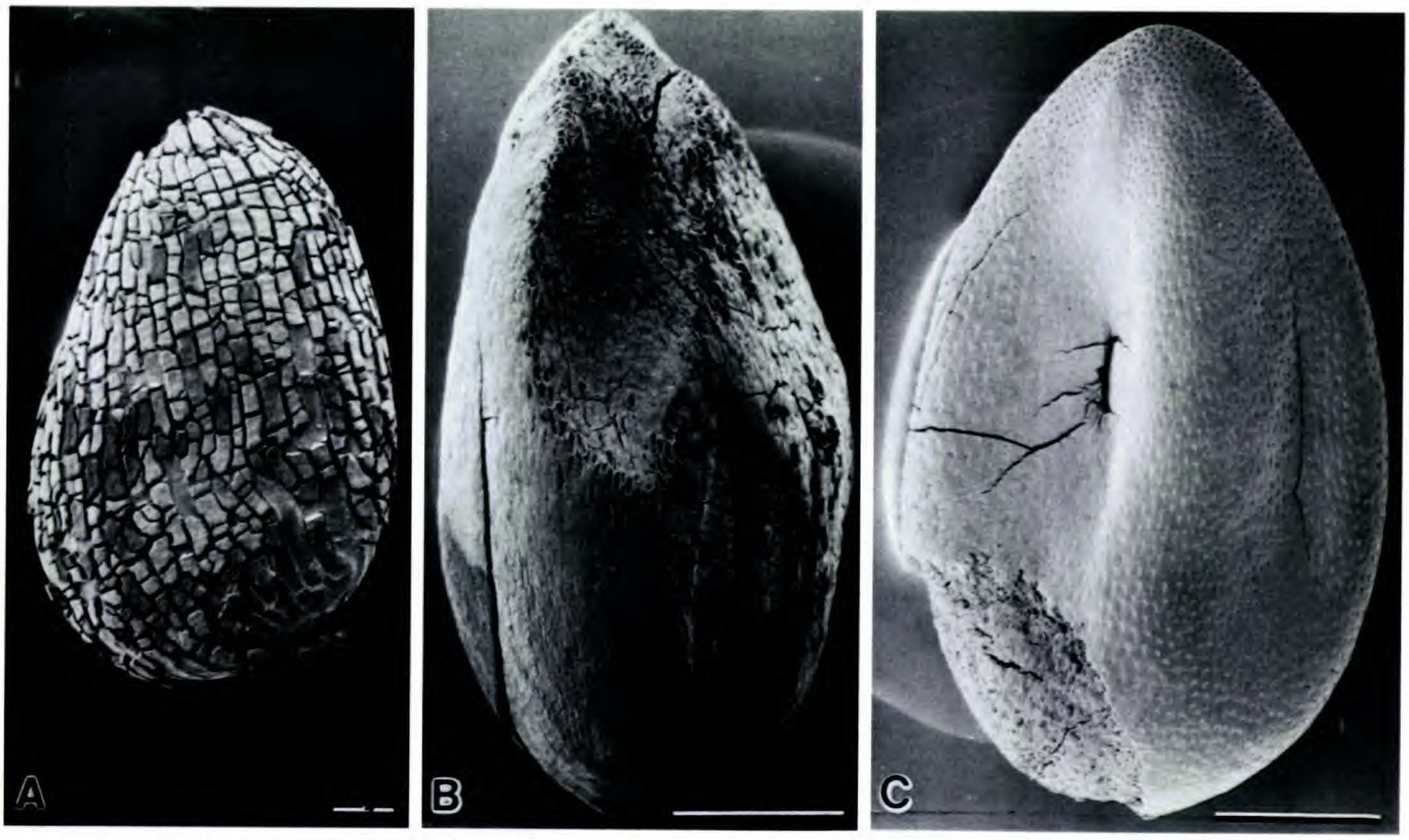

Figure 46. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxa 51, 52, and 53, Miscellaneous seeds. —A. Taxon 51, Miscellaneous seed type 1, small seed with characteristic exfoliating outer cell layer of seed coat; PP44678. —B. Taxon 52, Miscellaneous seed type 2, large seed with oblique fissure lines demarcating two presumed abortive seeds; PP45245. —C. Taxon 53, Miscellaneous seed type 3, large seed with finely pitted surface; PP45246. Scale bars: A = 100 μm; B, C = 0.5 mm.

than the fossil leaf assemblages described from the Ripley Formation (Berry, 1919, 1925), which are of early Maastrichtian age, and younger than the fossil leaf floras described from the Tuscaloosa Formation (Berry, 1919), which are of late Cenomanian age. Interpretations based on these and other leaf floras from southeastern North America, which range in age from late Cenomanian to early Maastrichtian, have suggested that the climate was wet and warm (ca. 25–30°C mean annual temperature) resulting in paratropical closed canopy forest (Upchurch & Wolfe, 1993; Wolfe & Upchurch, 1987; Wolfe, 1997). The mean annual temperature for the Middendorf leaf flora in particular was estimated at 23–25°C. Using the calculation of Wilf (1997) results in a mean annual temperature estimate of 26 ± 4°C.

The Allon flora is typical of Late Cretaceous mesofossil assemblages from the Atlantic Coastal Plain of North America in being dominated, both in terms of diversity of species, and in terms of abundance of specimens, by angiosperm remains. Flowers, fruits, and seeds of angiosperms far outnumber specimens of all other groups of plants combined. Conifers, primarily represented by fragments of leafy shoots, are next in abundance and are sufficiently common that they were almost certainly an important component of the original source vegetation. Sporophytes and gametophytes of mosses are not as frequent as the conifer remains, but they are not uncommon at this site. Ferns are the least abundant of the major plant groups in the Allon mesofossil assemblage. Nonconiferous gymnosperms (*Ginkgo*, cycads, Gnetales), sphenopsids, or lycopods have not yet been recognized. Also, no megaspores have been recovered from Allon.

This pattern in the representation of different major groups of plants contrasts strikingly with that at certain other Late Cretaceous localities from North America. For example, Late Cretaceous floras from distal floodplains on the North Slope of Alaska are dominated by ferns, cycadophytes, ginkgos, and conifers (Spicer, 1987). Similarly, the relatively poor representation of ferns in the Allon flora (both in diversity and abundance) is very different from the vegetation dominated by ferns and monocots in the Maastrichtian Meteetsee Formation of Wyoming (Wing et al., 1993). A primary factor in accounting for these differences may be marked latitudinal differences in climatic conditions.

Among the angiosperms at the Allon site, four taxa comprise more than 75% of specimens recovered. In decreasing abundance they are: ovate fruit (taxon 40), flower with a spindle-shaped inferior

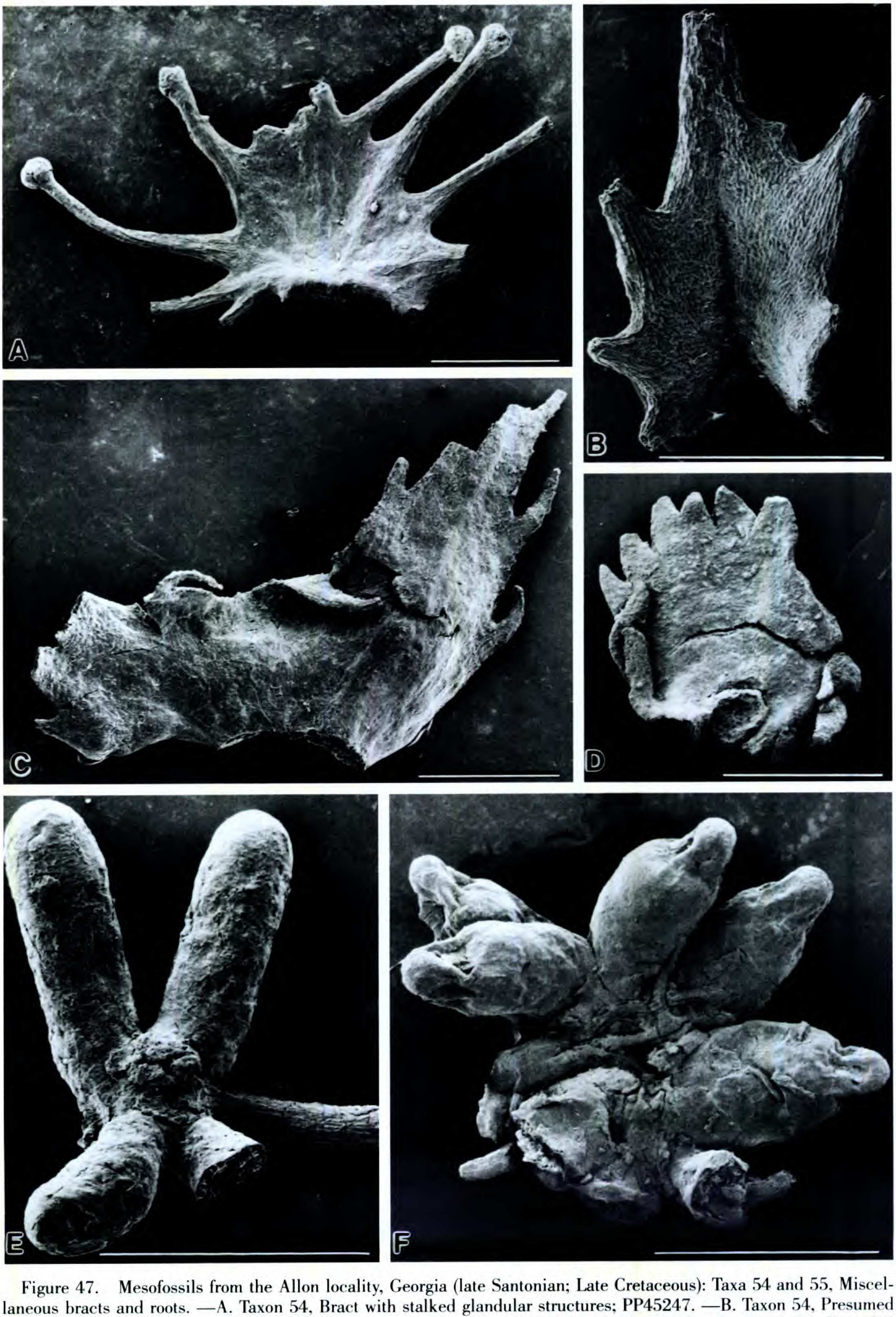

Figure 47. Mesofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxa 54 and 55, Miscellaneous bracts and roots. —A. Taxon 54, Bract with stalked glandular structures; PP45247. —B. Taxon 54, Presumed bract with acute pinnate lobes; PP45248. —C. Taxon 54, Asymmetrical bract; PP45249. —D. Taxon 54, Rounded bract with dentate margin; PP45250. —E. Taxon 55, Root with presumed nodules; PP45251. —F. Taxon 55, Root with presumed nodules; PP45252. Scale bars = 1 mm.

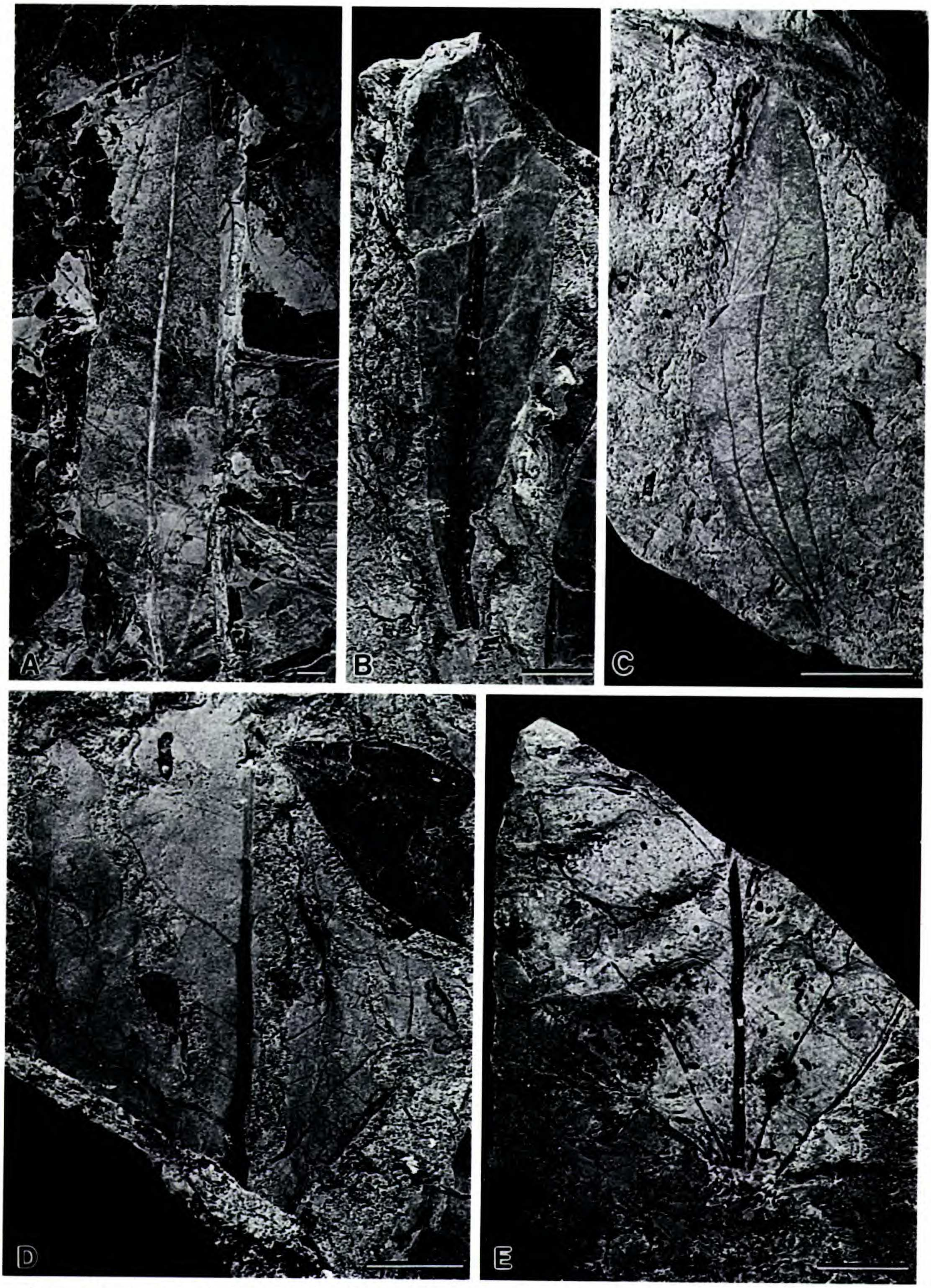

Figure 48. Macrofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxa 56–60, Miscellaneous dicot leaves, light micrographs. —A. Taxon 56, Dicot leaf type 1, macrofossil; PP45381. —B. Taxon 57, Dicot leaf type 2, macrofossil; PP45382. —C. Taxon 58, Dicot leaf type 3, macrofossil; PP45383. —D. Taxon 59, Dicot leaf type 4, macrofossil; PP45384. —E. Taxon 60, Dicot leaf type 5, macrofossil; PP45385. Scale bars = 10 mm.

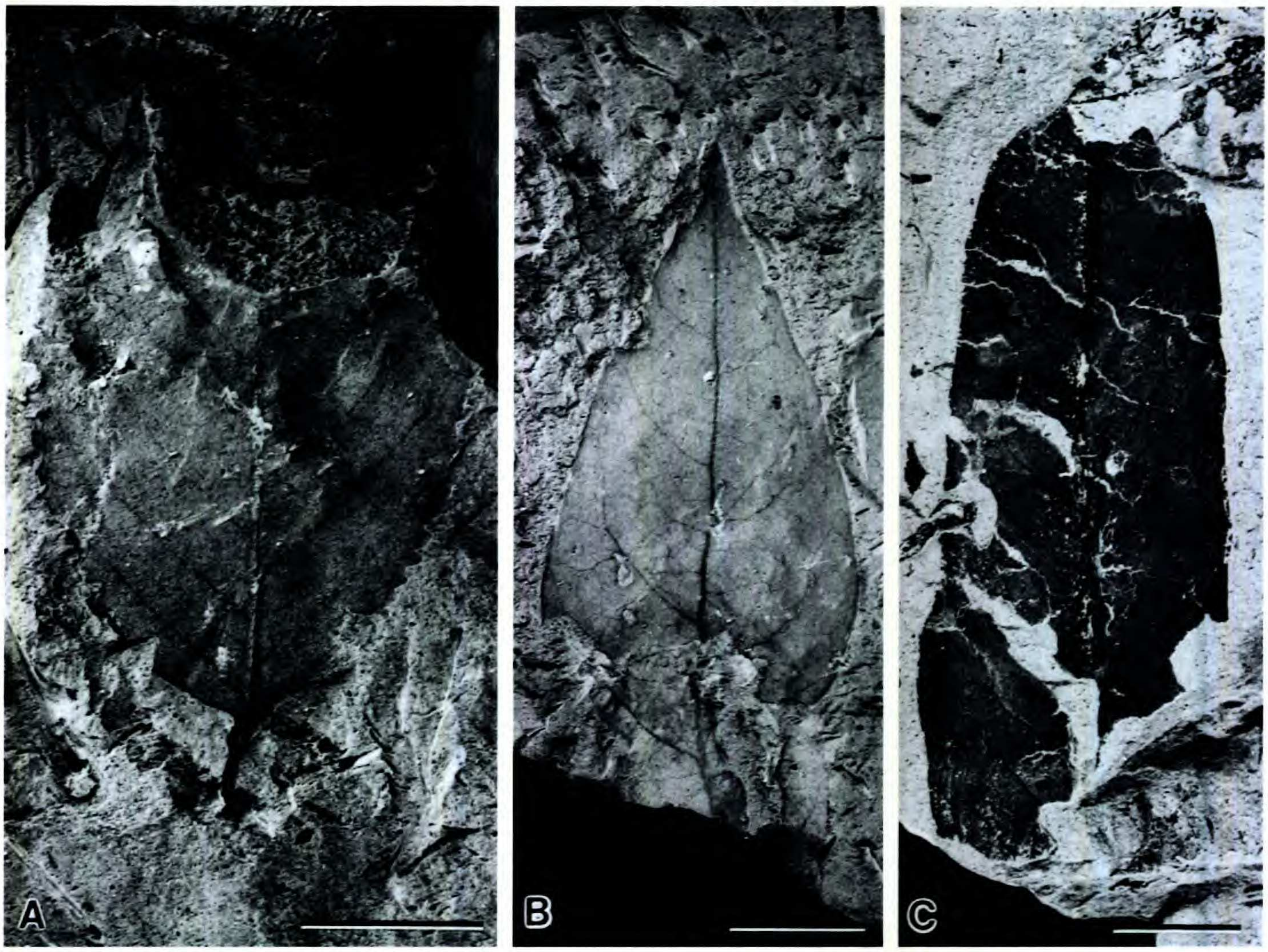

Figure 49. Macrofossils from the Allon locality, Georgia (late Santonian; Late Cretaceous): Taxa 61–63, Miscellaneous dicot leaves, light micrographs. —A. Taxon 61, Dicot leaf type 6, macrofossil; PP45386. —B. Taxon 62, Dicot leaf type 7, macrofossil; PP45387. —C. Taxon 63, Dicot leaf type 8, macrofossil; PP45388. Scale bars = 10 mm.

ovary (taxon 31), flower with lobed petals (taxon 32), and *Antiquacupula sulcata* (taxon 21). The abundance of *Antiquacupula* and *Protofagacea* (the sixth most abundant taxon) implies that Fagaceae sensu lato were an important element in the source vegetation. Probable taxodiaceous conifers are the fifth most abundant element in the Allon flora and were probably also common. The relative paucity of ferns, and good representation of mosses, may also indicate a relatively poorly developed understory vegetation. More detailed analyses of the diversity and abundance of different taxa in the Allon flora and other mesofossil assemblages are currently under way (Lupia, work in progress). These studies will compare the composition of the Allon mesofossil assemblage with the palynoflora and macroflora at the same site.

Preliminary results from the Allon locality (Lupia, work in progress) indicate that plants represented in the mesofossil assemblage are often not recognized in the dispersed pollen spore flora. The diversity of plants represented as mesofossils is also much greater than the diversity of plants represented as macrofossils (Table 1). Only 11 types of leaf macrofossils have been recognized at the Allon site, whereas the mesofossil assemblage records between 40 and 50 distinct botanical entities, including some (e.g., the mosses) that would be unlikely to be represented in the macroflora even under the most favorable circumstances. It is also interesting that while only two types of leaf macrofossil are abundant at the site, seven taxa are as abundant in the mesofossil assemblage (Table 1).

Mesofossil assemblages at Allon, as is typical of localities on the Atlantic Coastal Plain of North America, contain a mixture of lignified and charcoalified specimens. Pollen is frequently better preserved in lignified material, whereas charcoalification generally preserves finer anatomical and morphological details. The quality of preservation of the charcoalified material from the Allon flora suggests that it was not transported extensively prior to deposition and is consistent with preservation under quiet, near allochthonous, conditions. Actualistic studies do, however, show that fossil plant structures preserved as charcoal are significantly

Table 1. Composition of the Allon flora from the Late Cretaceous (late Santonian) of central Georgia, based on macrofossils and mesofossils. Unless otherwise indicated, fossils are angiosperms *incertae sedis*. Relative abundance is based on over 11,000 mesofossil specimens counted from 12 samples (Lupia, in prep.). Rank follows Spicer and Hill (1979) but combining the "rare" and "rare or localized" categories; asterisk (*) preceding rank indicates taxa with > 1000 specimens. Mesofossil taxa not appearing in the 12 samples were considered "very rare." Relative abundance for macrofossils is indicated in italics, based on an estimate of the approximately 100 blocks in our collection.

Taxon or structure	Organ	Relative abundance
1. *Eopolytrichum antiquum* Konopka, Herendeen, Smith Merrill & Crane (Polytrichaceae)	sporophyte capsules and gametophytes	rare
2. *Campylopodium allonense* Konopka, Herendeen & Crane (Dicranaceae)	sporophyte capsules and gametophytes	rare
3. cf. *Boodlepteris* Gandolfo, Nixon, Crepet & Ratcliffe (Gleicheniaceae)	pinnules	common
4. Fern leaf type 1	pinnules	common
5. Fern leaf type 2, macrofossil	frond fragment	*very rare*
6. Conifer foliage type 1 (cf. *Brachyphyllum*) macrofossil	shoot with leaves	*very rare*
7. Conifer foliage type 2, macrofossil	shoot with leaves	*very common*
8. Conifer foliage type 3 (cf. Taxodiaceae)	shoots with leaves	abundant
9. Conifer foliage type 4 (cf. *Brachyphyllum*)	shoots with leaves	common
10. Conifer pollen cone and dispersed cone scales	cone and dispersed cone scales	common
11. cf. *Detrusandra* Crepet & Nixon (Magnoliales)	flowers	very rare
12. *Mauldinia* sp. Drinnan, Crane, Friis & Pedersen (Lauraceae)	inflorescence units and flowers	rare
13. Trimerous staminate flower (cf. Triuridaceae)	staminate flowers	very rare
14. Tricarpellate flower (cf. monocots)	flowers	very rare
15. Monocot leaf type 1, macrofossil	leaf	*very rare*
16. Monocot leaf type 2, macrofossil	leaf	*very rare*
17. *Allonia decandra* Magallón-Puebla, Herendeen & Endress (Hamamelidaceae)	flowers and associated seeds	rare
18. Flower with apically connate stamen connectives (cf. Hamamelidaceae)	flower	very rare?
19. Capitate inflorescence (cf. subfamily Altingioideae, Hamamelidaceae)	inflorescences and pistillate flowers	very rare
20. *Protofagacea allonensis* Herendeen, Crane & Drinnan (Fagaceae sensu lato)	staminate inflorescence units and flowers, fruits, and cupules	abundant
21. *Antiquacupula sulcata* Sims, Herendeen & Crane (Fagaceae sensu lato)	staminate and bisexual flowers, fruits, and cupules	*abundant
22. *Caryanthus* sp. Friis (cf. Juglandales/Myricales)	flowers	very rare
23. Normapolles flower type A (cf. Juglandales/Myricales)	flower	very rare
24. *Bedellia pusilla* Sims, Herendeen, Lupia, Christopher & Crane (cf. Betulaceae)	staminate flowers	very rare
25. *Parasaurauia allonensis* Keller, Herendeen & Crane (Actinidiaceae)	flowers	rare
26. Flower with stellate trichomes, type 1 (cf. Ericales)	flowers	rare
27. Flower with stellate trichomes, type 2 (cf. Ericales)	flowers	very rare
28. Fruits with large peltate trichomes (cf. Ericales)	flowers	rare
29. Pentamerous flower with inferior ovary	flowers	very rare
30. Pentamerous flower with semi-inferior ovary	flowers	very rare

Table 1. Continued.

Taxon or structure	Organ	Relative abundance
31. Flower with spindle-shaped inferior ovary	flowers and fruits	*abundant
32. Flower with lobed petals	flowers	*abundant
33. Trimerous flowers with numerous coarse trichomes	flowers	very common
34. Capitate inflorescence of pentamerous flowers	inflorescence and flowers	very rare
35. Flower with pentamerous perianth and trimerous gynoecium	flowers	abundant
36. Flower with pentamerous calyx composed of thick valvate sepals	flowers	rare
37. Slender epigynous flower	flowers	very rare
38. Epigynous flower with spherical ovary	flowers	very rare
39. Flower with very broad perianth parts and coarse fimbriate trichomes	flowers	very common
40. Ovate fruit	fruits	*abundant
41. Bicarpellate superior fruit	fruits	very rare
42. Epigynous flower with rounded sepals	flowers	very rare
43. Pentamerous flowers with bracteoles	flowers	very rare
44. Immature bicarpellate fruit	fruit	very rare
45. Inflorescence with trimerous flowers	inflorescence with flower buds	common
46. Strobiloid spicate axis	axis	very rare
47. Spherical capitate inflorescence	inflorescence	very rare
48. Miscellaneous axes with attached leaves/bracts, type 1	axis	very rare
49. Miscellaneous axes with attached leaves/bracts, type 2	axis	very rare
50. Axis with pinnate bracts	axis	very rare
51. Miscellaneous seed type 1	seed	very rare
52. Miscellaneous seed type 2	seed	rare
53. Miscellaneous seed type 3	seed	very rare
54. Bract	bract	very rare
55. Root with nodules?	roots	very rare
56. Dicot leaf type 1, macrofossil	leaf	*abundant*
57. Dicot leaf type 2, macrofossil	leaf	*abundant*
58. Dicot leaf type 3, macrofossil	leaf	*common*
59. Dicot leaf type 4, macrofossil	leaf	*very rare*
60. Dicot leaf type 5, macrofossil	leaf	*rare*
61. Dicot leaf type 6, macrofossil	leaf	*very rare*
62. Dicot leaf type 7, macrofossil	leaf	*very rare*
63. Dicot leaf type 8, macrofossil	leaf	*very rare*

smaller than they were in life (McGinnes et al., 1976; Scott, 1989; Herendeen, 1991b), and care must be used in comparing the absolute dimensions of fossils preserved in this way (Lupia, 1995). In a study of charcoalification of angiosperm reproductive structures Lupia (1995) documented shrinkage of 14% to 47%, with substantial variation among plant organs studied.

The proportion of mesofossils preserved as charcoal or lignite varies among, and sometimes within, sites. Some localities are dominated by lignified specimens while others consist almost entirely of charcoal, formed as a by-product of natural fires. Interestingly, at Allon, as at other localities on the Atlantic Coastal Plain, the mode of preservation sometimes varies by taxon. Some taxa are represented exclusively, or almost exclusively, by charcoalified specimens, others are represented by both charcoalified and lignified specimens, while others are represented by only lignified material. These differences could represent a variety of factors, such as differences in phenology relative to (?seasonal) fire patterns, or the effects of habitat variation resulting in differences in fire susceptibility, and deserve further investigation including actualistic studies in contemporary plant communities subject to forest fires. At the Allon locality the preservation of some specimens of almost all taxa as charcoal indicates that fire may have been an important factor contributing to frequent disturbance of the source plant community. The extent to which such fires may have been a function of a particular climatic regime, thereby introducing potential large-scale biases into studies of the mesofossil record, remains to be determined.

Previous publications on plants from the Allon locality have presented detailed descriptions and analyses of relationships of specific fossil taxa. In many cases the excellent structural details preserved in these fossils have made it possible to carefully integrate paleontological and neontological data and document the presence of synapomorphies of extant groups of families, subfamilies, or even genera (e.g., Keller et al., 1996; Magallón-Puebla et al., 1996). Such studies have substantially modified previous estimates of the time of differentiation of several groups of extant angiosperms (e.g., Hamamelidaceae: Magallón-Puebla et al., 1996; Fagaceae sensu lato: Herendeen et al., 1995; Sims et al., 1998).

The combined effect of this work, together with information from other mesofossil localities, has been to modify our current understanding of the "modernization" of the angiosperm flora through the Late Cretaceous. Syntheses of data from dispersed fossil pollen (Muller, 1981, 1984) suggest that most extant angiosperm families differentiated during the latest Cretaceous or Early Tertiary, but the rapidly accumulating evidence from mesofossils, with the increased systematic precision provided by information on flowers and fruits, indicates that many extant angiosperm lineages were already differentiated at the level of family, or even genus, by the Turonian-Campanian. Continued study of rich mesofossil assemblages such as Allon, other localities in southeastern North America (Herendeen & Crane, work in progress), the Potomac Group localities in Virginia and Maryland (Crane, Friis & Pedersen, work in progress), the Crossman site in New Jersey (Crepet & Nixon, work in progress), the Åsen flora in southern Sweden (Friis, Pedersen & Schönenberger, work in progress), the numerous localities in Portugal (Friis, Pedersen & Crane, work in progress), and recently discovered mesofossil floras in Asia (Frumin & Friis, work in progress; Takahashi, Crane & Ando, work in progress) is certain to further expand the spectrum of angiosperm lineages that can be recognized.

Mesofossil assemblages such as Allon also offer to provide new and valuable information about ferns (Gandolfo et al., 1997b; Herendeen & Skog, 1998), cheirolepidiaceous conifers (Srinivasan, 1995), and other pteridophyte and gymnosperm taxa (Pedersen et al., 1989, 1993). Especially interesting is the new information on Late Cretaceous fossil mosses (Konopka et al., 1997, 1998), which suggests that careful examination of other mesofossil floras may substantially expand current knowledge of the bryophyte fossil record (e.g., Crandall-Stotler et al., 1996).

CONCLUSIONS

A rapid increase in our knowledge of Cretaceous mesofossil assemblages is contributing to a substantially improved understanding of the composition of Cretaceous vegetation, and providing new and more precise insights into the phylogenetic relationships and evolutionary significance of Cretaceous plants. However, the full wealth of systematic and paleoecological information that can be obtained from these assemblages is only just beginning to be exploited. A very large number of new taxa remain to be described in the mesofossil assemblages that are already known, and many more mesofossil assemblages will be discovered as additional areas are explored and the techniques of bulk sieving are applied more widely.

The mesofossil approach, which so far has been mainly applied to studies of Cretaceous and Tertiary sediments, also holds great promise for studies of other time periods and a broader range of taxonomic groups. For example, exquisitely preserved mesofossils from early Devonian sediments are already providing important new information on early land plants (Edwards, 1997), while the recognition of such floras from late Paleozoic and early Mesozoic could be extremely helpful in studies of a variety of pteridophyte and gymnosperm groups.

The study of mesofossils has already resulted in a much improved knowledge of Cretaceous angiosperms. However, much work remains to be done in terms of describing the full range of taxa present, characterizing the individual plants, and understanding their relationship to their living relatives. The documentation of complete assemblages, such as we have attempted here for the Allon flora, combined with detailed studies of individual fossil plants, has much to contribute to a more refined understanding of early angiosperm evolution and global environmental change in terrestrial environments during the Cretaceous.

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